EIGHT

Ecosystems Past

Vegetation Prehistory

CONSTANCE I. MILLAR and WALLACE B. WOOLFENDEN

Introduction

Historical accounts are usually rendered as narratives that chronicle a sequence of events over time and space. While the story is important, history is as much about process (how things came to be) as pattern (the story). Understanding processes of change is one important way we can learn from the past and, in the context of vegetation and ecosystems, benefit conservation and stewardship. Over long expanses of time, three primary forces have influenced the development of terrestrial ecosystems across California's landscape. The first is geologic, with processes that affect vegetation at long and short time scales. Geologic settings are the stage on which regional ecosystems and vegetation develop. Over millions of years and through complex tectonic processes, landforms such as continental margins, inland seas, mountain ranges, upland plateaus, valleys, and basins were created and destroyed. In contrast to long, slow geologic processes, for example, volcanic eruptions, earthquakes, and tsunamis occur in geologic instants, exerting significant and long-lasting effects on vegetation. Geologic processes strongly affect the second primary force of historical ecosystem change: climate. If geology is the stage for vegetation development, climate is the director. The latitude of continents dictates atmospheric conditions; proximity to oceans and the configuration of continents relative to oceans confer distinct regional climates; high elevations are cooler than low elevations; and mountains focus cloud formation while creating rain shadows along their lee slopes.

Less well understood are the diverse forces and relentless nature of climate change. In that climate can be described as the average of weather variations, this average is wholly dependent on a particular time frame. As the time frame is shifted back or lengthened, climates are significantly different from present. While public awareness of anthropogenic climate change in the twentieth and twenty-first century has increased, understanding of the role of natural climate change over a longer (prehistoric) period of time has not. A widespread perception remains that climates started to change only in the late twentieth century. To the contrary, climates have been changing continually over historical time. The natural condition is for climates to be expressed at multiple, hierarchic levels, with interannual regimes (e.g., El Niño/

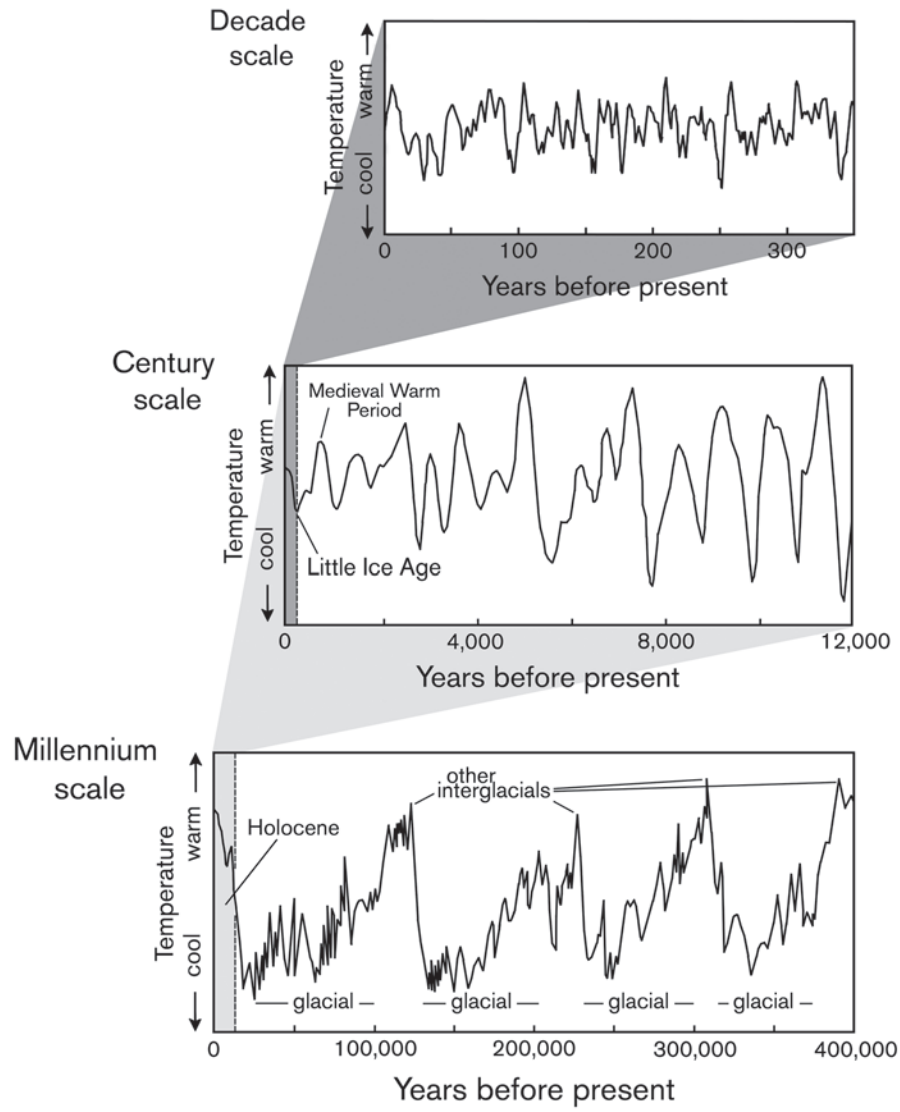

FIGURE 8.1 Global temperature cycles showing the nested nature of climate modes at different temporal scales.

TOP: Decadal cycles driven by ocean circulation and sea surface temperatures. Source: Biondi et al. 2001.

MIDDLE: Centennial cycles driven by solar variability. Source: Bond et al. 2001.

BOTTOM: Millennial cycles driven by changes in earth's orbit relative to the sun. These and other cycles interact continually and, in combination, result in ongoing changes in earth's natural climate system. Source: Petit et al. 1999.

La Niña) nested in decadal modes (e.g., Pacific Decadal Oscillation), these nested within multicentury modes (e.g., Bond cycles that influenced the Medieval Climatic Anomaly and the Little Ice Age) (Mann et al. 2009), and these nested within even longer-term multimillennial cycles (e.g., glacial and Milankovitch cycles; Figure 8.1).

Diverse physical mechanisms called "forcing factors" drive these cycles at different scales. For instance, variations in ocean-circulation and sea-surface temperatures drive interdecadal and multidecadal changes; shifts in solar activity force centennial climate modes; and variability in Earth's orbit and relationship to the Sun control the long glacial-to-interglacial cycles of the past two million years. While these are quasi-independent, the drivers interact, and climate at any one moment is expressed as the cumulative effect of all modes acting together. This results in changes that can be gradual and directional, episodic or reversible, characterized by abrupt changes and extreme events, and/or chaotic patterns. Ecosystems respond to climate changes at all of these scales, varying in extent with the magnitude and nature of change. Greenhouse gas emissions and other human influences on climate are superimposed on the ongoing natural forces of climate change.

Genetic adaptation is the third great force of change on vegetation over time. If geologic and climatic conditions provide the stage and direction for species to play out ecological dramas, evolutionary forces alter the inherent nature of the biota. Forced by geologic setting and climate, determinate processes such as natural selection drive adaptive evolution, wherein populations change in their genetic capacity to

Photo on previous page: The current landscape of the high Sierra Nevada bears witness to the cumulative effects of past geologic, climatic, and vegetation epochs. Here along the eastern escarpment of Rock Creek Canyon, pastels reveal glacial cirques, horns, and arêtes that were etched by long-gone Pleistocene glaciers along the range crest south of Mono Pass. Tiny, late Holocene glaciers, sharing no relation to their Pleistocene forebears, perch tenuously on the highest cirque headwalls as remnants from the recent Little Ice Age. Similarly, Marsh Lake in the foreground reflects wetlands and wetland vegetation relictual from the cooler, relatively wetter Little Ice Age. Subalpine forests of whitebark pine and occasional mountain hemlock fringe Marsh Lake in high density relative to their sparser woodland condition during recent centuries past. Deeper in the past, more than eleven thousand years ago, no forests—or vegetation at all—were present in this high canyon. Instead, hundreds-of-meters-deep ice formed a massive ice cap over the high Sierra Nevada during the coldest part of the last glacial period. Painting by Wallace Woolfenden.

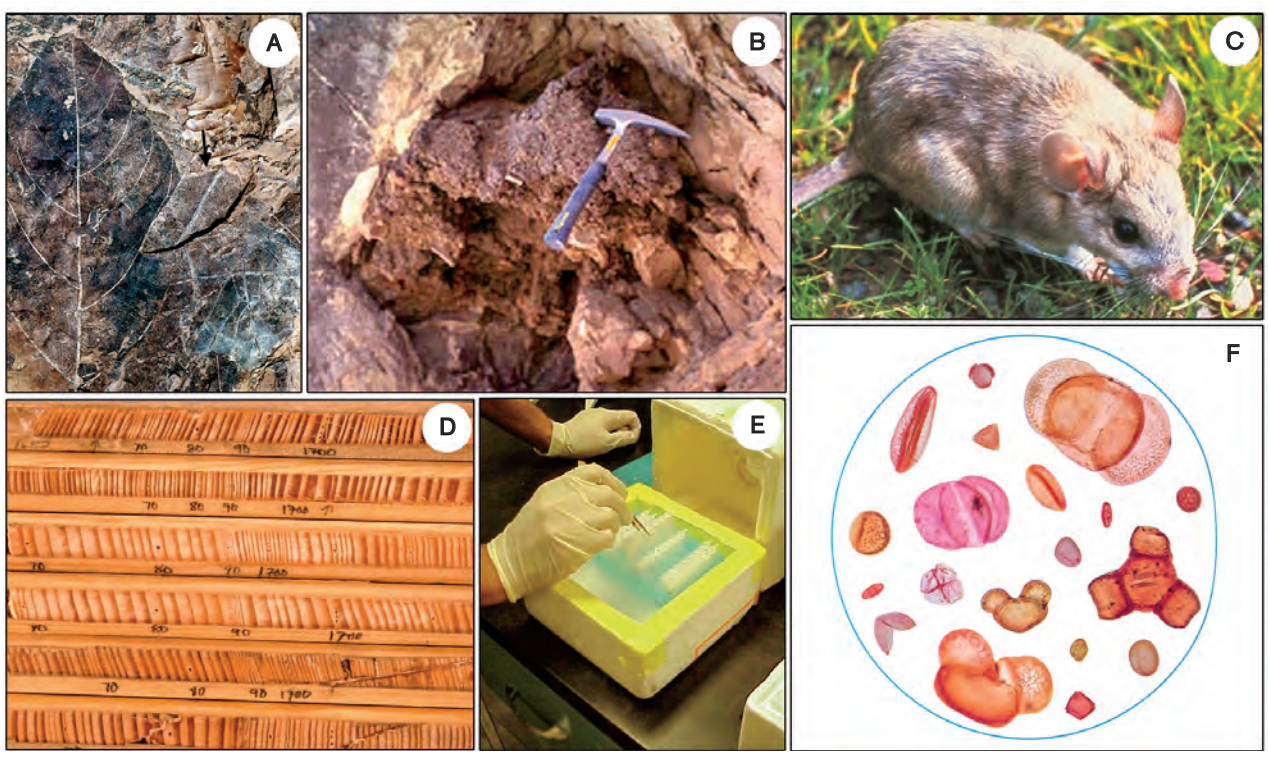

FIGURE 8.2 Diversity of proxies used for reconstructing historical vegetation.
Photos: (A) Diane Erwin, (B) U.S. Geological Survey, (C) from U.S. Geological Survey National Research Program, (D) Henri Grissino-Mayer, <http://web.utk.edu/~grissino/treering-gallery1>, (E) Paul Hodgskiss, and (F) modified from Mehringer 1967.

A Impression fossil of buckeye (*Aesculus* spp.) from Paleogene Chalk Bluffs Flora, western Sierra Nevada.

B Indurated midden constructed by bushy-tailed packrats (*Neotoma cinerea*).

C Desert packrat (*Neotoma lepida*).

D Increment cores from tree-ring extraction of ponderosa pine (*Pinus ponderosa*) stems in Arizona.

E DNA extracts from fresh foliar tissues for phylogenetic reconstruction.

F Pollen grains from a composite plate of Pleistocene age, Las Vegas Valley, Nevada.

survive and thrive in given locations and climates through reproductive and survival advantages conferred on fitter individuals. Stochastic processes, by contrast, of mutation, gene flow, and genetic drift create and alter the raw material of genetic diversity on which natural selection acts. Over long and short time spans, new life is formed as populations diverge into races, and races evolve into species. Individual mortality, population extirpation, and species extinction play significant roles by removing genotypes in determinate and stochastic ways. Geologic and climatic events, such as uplift of mountains, retreat of seas, and abrupt cold or warm periods, further drive divergence among taxa, forcing the evolution of remarkable biodiversity we inherit on Earth now.

Why does it matter in the study of California ecosystems to understand history and the forces of change that underlie vegetation development? Similar to understanding family ancestry, there is the sheer delight at knowing our regional history. For its role in revealing and explaining current conditions, history informs and clarifies. For fixing what might be broken (ecological restoration), and for anticipating and managing the future (climate projections and adaptation), the chronicles of history comprise essential course materials. History reminds us that California's diverse ecosystems today are just the leading edge of a long chain of species and ecosystems that has flowed across the region's shifting landscapes under constantly changing climates.

Reconstructing the Past: Methods of Historical Ecology

The methods of historical studies differ fundamentally from those focused on modern issues because the past cannot be repeated and experimentation is impossible (Bradley 1999). More akin to detective work, interpretation of historical process is by inference based on traces and relicts that remain, and by comparing effects of historical events across different places and times. Reconstructing historical conditions is the central task of paleoecology, whether to write the narrative for a region or to interpret the forces of change. Many sources of evidence for reconstructing terrestrial vegetation and ecosystem processes are available, depending on the environmental context and time period of interest, including molecular, organic geochemical, pollen, spores, algae, invertebrate remains ("microfossils," e.g., insects, freshwater/marine organisms, foraminifera, and dinoflagellates), charcoal from meadow, bog, or lake sediments; plant parts (micro and macrofossils) from woodrat middens; annual growth rings and fire scars from perennial woody trees and shrubs; permineralized and impression plant fossils; plant remains in archeological sites; and archival records, including ethnographic and recent historical documents, oral histories, sketches, and photographs (Figure 8.2). Each proxy has biases (TAPHONOMY, preservation, etc.), and the most robust reconstructions integrate multiple lines of evidence.

In addition to identifying and describing former plant species, including their biogeography and assemblages, historical ecologists seek information about past forces of change, geology, climate, and evolution. Thus reconstruction of environmental and genetic contexts commonly is also attempted. Many archives that reflect historical processes ("proxies") of climate and geology exist, including sediment and chemistry analysis from lake and bog cores; assessment of bedrock and overburden exposures and orientations; ash and tephra deposits; surface fluvial remains; glacial moraine orientations; and ice archives from glacial cores (Bradley 1999). Indirect reconstruction of climate is also made from assessment of plants and animals living at a historical time, basing inferences on correlations of modern taxa and climate ("climate analogs") or through analysis of plant physiognomy (Wolfe 1995).

Methods for assessing evolutionary forces traditionally focused on interpreting changes in plant parts (morphology) and their inferred function over time. These methods particularly emphasized reproductive structures, which tend to be under strong natural selection, thus conservatively representing phylogeny. Macrofossils have been especially important for understanding evolution prior to the Quaternary, where more continuous samples of microfossils are available for evolutionary assessment. The advent of biochemical and molecular techniques during recent decades, however, has revolutionized interpretation of evolutionary history in plants and animals, both through phylogenetic reconstructions of DNA and direct assessment of ancient DNA from fossil material. Recent literature on California plant and animal evolution contains many revisions from molecular analyses of phylogenetic relationships and times of divergence (Calsbeek et al. 2003). This chapter focuses on California's geologic and climatic history, highlighting the shifts in climate, landscape, and the concomitant rise and fall of California's diverse assemblages over deep geologic to recent times.

Misty Origins: Mesozoic Ecosystems (252–66 Ma)

Over multimillennia prior to the Cenozoic (>66 million years ago, Ma; Figure 8.3) and including the Mesozoic Era (252 Ma–66 Ma), the western margin of what is now North America constituted a long coastline abutting major oceans. The location of that shoreline, the presence and absence of offshore land masses (island arc volcanoes), the transgression and regression of a great inland seaway in midcontinent, and uplands that are now California changed greatly over time (Figure 8.4; Blakey 2008). However, California was under water much of this time. Exceptions to this are island relicts that are now land components mostly in northwestern California, and a varying width of land along the California–Nevada border region. Thus the early history of plants in California has to do with their origins elsewhere, their occasional appearance on fragmentary land masses, and their expansion throughout the California region with the emergence of greater amounts of land in the early Cenozoic.

Movements of the southwestern regions of the continent in this period are important to the climate and environmental context for plants. These regions passed first through latitudes lower than present earlier in time, then later through latitudes higher than present (in the mid-Cretaceous), arriving near their present latitudes by the end of the Mesozoic (Blakey 2008). Major mountain-building episodes (the Nevadan and Sevier orogenies) between 200 Ma and 70 Ma resulted in extensive north-south volcanic chains, with exposures in the Klamath Ranges, Sierra Nevada, Basin and Range Province, Mojave Desert, and Peninsula Ranges, as well as intrusion of magma, mostly granitic, far underground in batholiths (later uplifted as the Sierra Nevada) (Harden 2004). Much of the exposed portions of eastern California and the region of today's Great Basin became elevated plateaus (steppe) built by this volcanic activity (DeCourten 2003, Mix et al. 2011). Reflecting the changing latitudinal and altitudinal situations over time, early climates during this period ranged from tropical (annual temperatures 10°C warmer than present) to cool temperate, although humidities were relatively high and rain shadows mostly lacking (Figure 8.5). Although subalpine and possibly alpine conditions existed, hot arid desert did not.

Several ancient GYMNOSPERM lineages, such as cycads (Cycadaceae), redwoods (Taxodiaceae), and ginkgos (Ginkgoaceae), had their heyday during the Mesozoic (Miller 1977). Many members of the latter two families extended across the Northern Hemisphere, including western North America. Taxodiaceous taxa appeared ~245 Ma, with redwood (*Sequoia*) and relatives dating to ~200 Ma. Giant sequoia (*Sequoiadendron*) is not known from the Mesozoic, although the diversity of forms appearing after 66 Ma suggests that it had earlier origins. By ~200 Ma, modern conifer families are recognizable. Pinaceous conifers underwent an extensive radiation during the early Cretaceous (~145 Ma), lagging behind other conifer families (Miller 1976). To date, among extant genera of the pine family (Pinaceae), only pines (*Pinus*) are recognized in the Cretaceous, the other genera appearing later in the Paleogene (Smith and Stockey 2001). Early forms of Pinaceae appeared by 150 Ma, although their radiation lagged those of other conifers (Miller 1976). *Pityostrobus*, a group of Pinaceae taxa that disappeared by 33–30 Ma, and pines are among the oldest records for this family. In addition to gymnosperms, ferns (including horsetail, *Equisetum*) radiated and expanded worldwide starting ~150 Ma.

Rapid diversification of ANGIOSPERM taxa began ~110 Ma, with almost exponential increase in taxonomic diversity (Crane et al. 2000). By this time, angiosperms were abundant on a worldwide basis, and by 66 Ma they had become the most diverse and floristically dominant group of plants, as evidenced by the composition of numerous MACROFOSSIL and pollen floras (Rettalack and Dilcher 1986). In North America the Cretaceous Western Interior Seaway separated two principal floristic provinces. The western province was distinguished by the abundance of *Aquilapollenites*, an early angiosperm pollen taxon resembling grains of modern sandalwood (Santalales) but likely representing a broad polyphyletic clade (Graham 1999). Closed-canopy forests of broadleaved evergreen angiosperms and conifer forests dominated in the warm humid environments, suggesting little seasonality and annual mean temperatures of 20°C to 25°C (Tiffney 1985). Middle latitude west-coast forests contained araucarian (monkey puzzle tree), rosid (rose), plantanoid (plane-tree), hamamelid (witch hazel) elements as well as species of birch (Betulaceae), elm (Ulmaceae), basswood (Tiliaceae), walnut (Juglandaceae), and sandalwood (Santalales) families. There is also evidence for a distinct continental margin floristic province based in part on pollen samples from California. This province is recognized by absence or low abundance of *Aquilapollenites*. Indications are that angiosperms first spread to California between 120 Ma and 100 Ma. During this and sub-

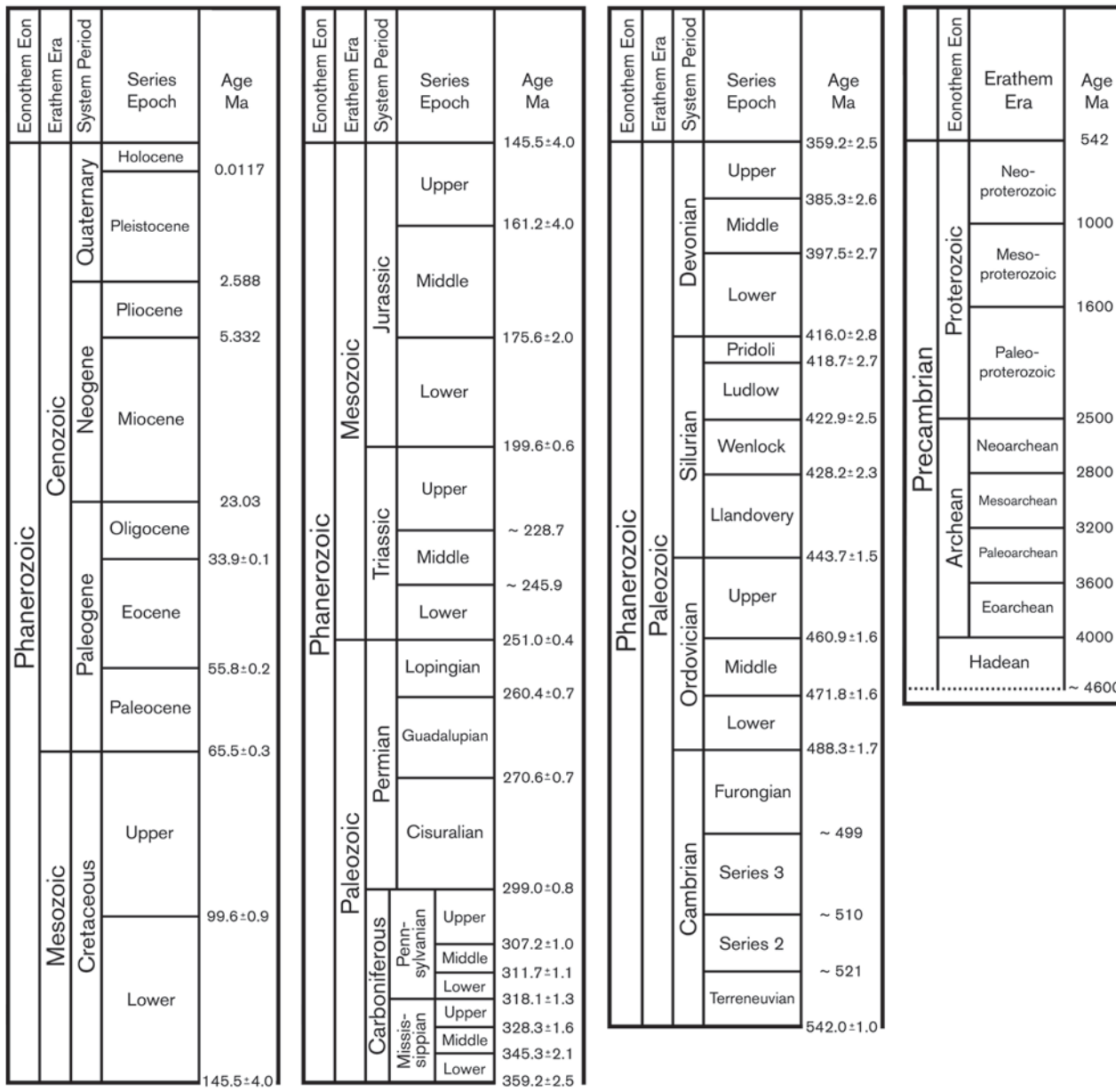

FIGURE 8.3 International stratigraphic time chart. Source: Cohen et al. 2013. Reproduced by permission © ICS International Commission on Stratigraphy, 2014.

sequent tens of millions of years, angiosperms in California appear to have been most extensive and abundant in coastal and fluvial environments, while conifers remained dominant in well-drained and upland areas (Upchurch and Wolfe 1993, Graham 1999).

The Cretaceous-Paleogene extinction at ~66 Ma marks one of the major extinction events (Pope et al. 1994, Schulte et al. 2010), with an estimated 40% loss of genera and 76% loss of species (Barnosky et al. 2011). This event has been attributed to the Chicxulub asteroid impact with Earth, but recent evidence suggests that the asteroid impact dealt only the final blow on ecosystems already under near-critical stress from climatic variability (Renne et al. 2013). During the one million years prior to asteroid impact, six abrupt shifts of >2°C in continental mean annual temperatures occurred, with the most dramatic oscillation involving a drop of 6°C to –8°C within one hundred thousand years prior to the impact. These alternated with two hot greenhouse events of about equal duration (Nordt et al. 2003; see Figure 8.5). In addition to nonavian dinosaurs and other animal lineages, many plant genera went extinct in this event, especially at locations near the impact site in Mexico (Wolfe and Upchurch 1986). Broad-leaved evergreen trees were at higher risk of extinction, whereas taxa with dormancy adaptations (e.g., deciduous leaves) fared better during the "impact winter" that followed (Wolfe 1991). Although California was relatively near the

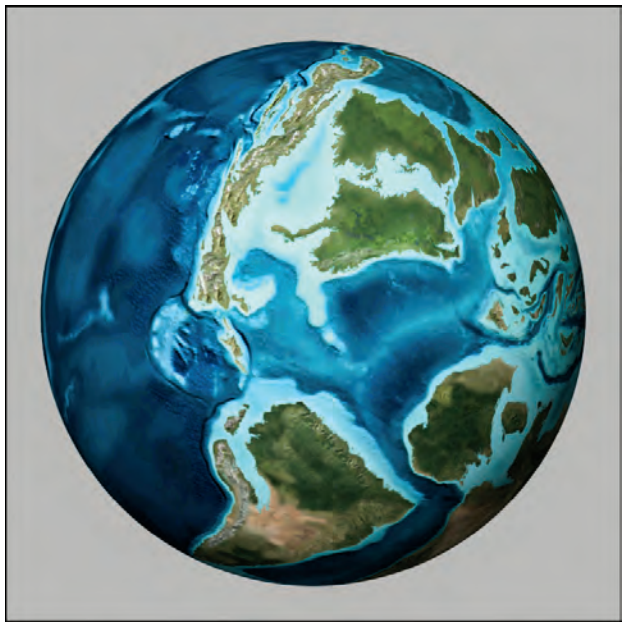

FIGURE 8.4 Paleogeography of North and South America, circa 90 Ma. An oblique Western Hemisphere view showing the Cretaceous Western Interior Seaway of midcontinent and the extensive mountain regions of western North America. Source: Blakey 2008.

impact site and would thus have been severely affected, no records from that time are firmly documented in the region. The best records are in western interior North America, in a zone from New Mexico north into Canada. Sites in this belt clearly indicate mass plant kills, with estimates of 50% to 75% extinction of earlier taxa.

Recognizable Taxa with Nonanalog Associations: Paleogene and Neogene (66–2.6 Ma)

During the early Paleogene the region at the eastern margin of California (now the Great Basin) was an elevated upland that drained to the west via rivers that flowed through California to the Pacific Ocean (DeCelles 2004; Cassel, Graham et al. 2009; Henry and Faulds 2010). A steep gradient existed along what is now the west slope of the Sierra Nevada, but the Sierra Nevada was not the major hydrologic divide that it is today. The uplands of what is now the Sierra Nevada were the western edge of a generally mountainous region that extended eastward and had summits reaching more than 2,750 meters (Henry and Faulds 2010, Mix et al. 2011). This region has been called the Nevadaplano as it reflects similar character to South America's Altiplano (DeCelles 2004).

About 40 Ma, through incompletely understood tectonic processes, changes in plate angles at the Pacific margin exposed the bottom of the continent to the underlying mantle's heat. Partial melting of the deep crust led to massive volcanic eruptions regionally. Exposure to deep heat also caused the continent to become less rigid and to thin and stretch. As this occurred, the entire Nevadaplano region subsided, like the domed top of a cake sinking as it comes from the oven. This subsidence and stretching marked the beginning of the evolution of internal drainage and the birth of the hydrologic Great Basin (DeCourten 2003). These events set the stage for a new era of mountain building. Continuous stretching caused blocks of the continental crust to tilt along faults, giving rise to fault-block topography that characterizes the present Basin and Range province, including the Sierra Nevada. Continued extension over the past thirty million years has more than doubled the amount of land between the western (Sierra Nevada) and eastern (Wasatch Mountains, Colorado Plateau) edges of the province, adding 400 kilometers of new landscape in the process (Thatcher et al. 1999). At about the same time, a major change occurred along the western margin of the continent that allowed the North American and Pacific plates to come into direct contact for the first time. Meeting of these two plates fundamentally changed the nature of the contact along western California, converting the boundary from one of subduction to lateral shear. This shear zone was the ancestral San Andreas fault system, which developed about 25–20 Ma (DeCourten 2003).

The history of the Sierra Nevada is closely linked to these tectonic events. Although mountains are known to have existed in the late Mesozoic where the present day Sierra Nevada lie, the prevailing view had been that this ancient range never gained elevation above ~2,000 meters and eroded to lowlands by the late Paleogene. Fault-block tilting of the past 10–5 Ma is believed to have created the high elevation of the modern Sierra Nevada. An increasing body of research, ranging from the composition of regional flora (Wolfe et al. 1998) to analysis of tectonics (Small and Anderson 1995, Mix et al. 2011), isotopic analysis of volcanic glass (Cassel, Graham et al. 2009), and age and distribution of Cenozoic lava flows (Cassel, Calvert et al. 2009; Henry and Faulds 2010), however, suggests that the Sierra Nevada achieved heights over 3,000 meters in the Paleogene and remained high through subsequent millennia to the present. This evidence does not suggest that the Sierra Nevada was exempt from effects of the extensional and faulting processes. The form, topography, and specific elevation of the modern Sierra Nevada were strongly influenced by those events, which appear to have taken place over the past three million years (Small and Anderson 1995).

Extensional forces that thinned the crust and generated basin and range topography also influenced topography in interior California. Especially in the Mojave Desert, faults formed as the crust stretched starting ~35 Ma. In many desert locations so much crust was displaced that older rocks below were exposed. The creation of faults via extension facilitated volcanic activity in the Mojave province, and many eruption centers arose around fault zones starting ~20 Ma. The Transverse Ranges derive their origin and orientation from lateral shear action along the Pacific and North American plates. The current Coast Ranges are geologically young and owe their origin to diverse and still poorly understood activities of plate contact as the lateral shear zone has increased (Harden 2004). Extension, fault-block tilting, and uplift contributed relief to this region, as did volcanic activity along the newly propagating San Andreas fault zone. Elsewhere at this time, in the interior mountains, forces remained that derived from subduction and included compression forces, bends in regional faults, and thrust uplifting. Between the ancient Sierra Nevada and the Coast Ranges lay the San Pablo Sea, a shallow inland water body, which dried at its north end ~9 Ma. A shallow sea persisted in the San Joaquin Valley to ~2 Ma (Harden 2004).

Climate of the Paleogene and Neogene paralleled the evolving landscape (Zachos et al. 2001). The interval began with

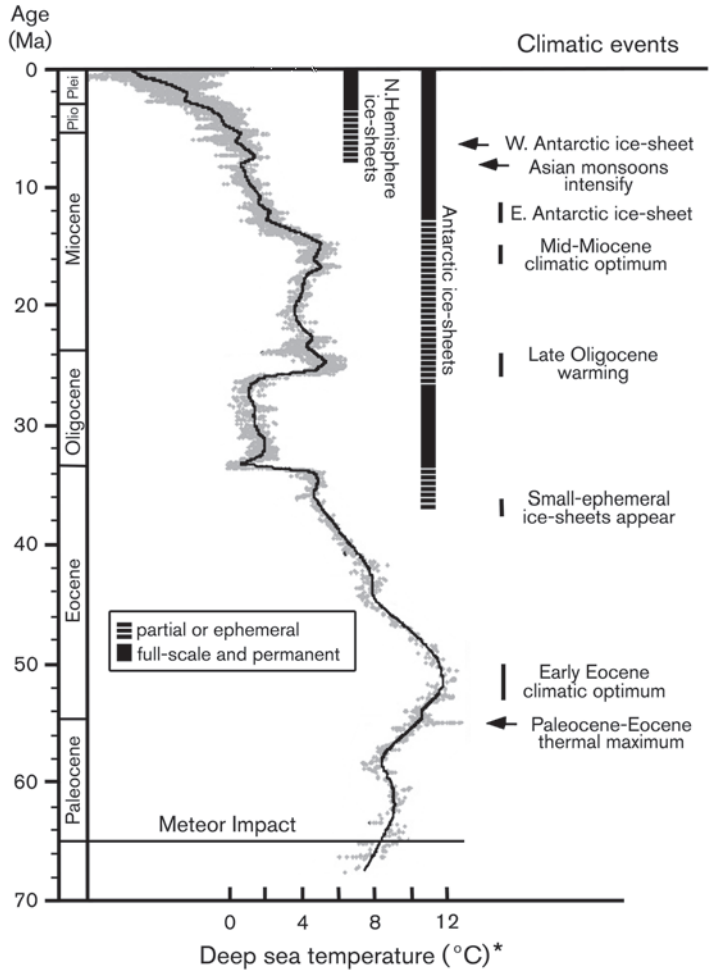

FIGURE 8.5 Major historical trends in global temperature and climatic, tectonic, and major biotic events over the past sixty-five million years. Temperature scale applies only to time before 35 Ma; deep sea values approximate sea-surface temperatures for high latitudes. Source: Modified with permission from Zachos et al. 2001.

a greenhouse climate regime, which had dominated the late Mesozoic. Two warm peaks included a hot spike at 65.5 Ma, attributed to asteroid impact, and a short hot pulse centered at 55.8 Ma, the Paleocene-Eocene Thermal Maximum (PETM), which lasted 170,000 years (see Figure 8.5; Zachos et al. 2008). During the PETM, global temperatures increased by 5°C to 10°C in fewer than twenty thousand years (20 ka). The cause of the PETM is still being debated but is widely attributed to spontaneous release of massive stores of methane hydrates from the ocean floor (Jenkyns 2003). A slight cooling trend followed that terminated with an abrupt and defining global cooling at 33.5 Ma, the Eocene-Oligocene event (Liu et al. 2009). A deep, 400,000-year-long glaciation followed, and temperatures at California latitudes during this period dropped by 6°C to 8°C. The Eocene-Oligocene event marked the return of a global icehouse regime that continues to present (see Figure 8.5). Ice-cap development began in Antarctica and only much later extended into the Northern Hemisphere. Global sea levels dropped by 70 meters, reflecting the buildup of polar ice. Two global warming periods interrupted the background icehouse conditions. Peaking at 17 to 15 Ma was the middle Miocene climatic optimum, after which global temperatures gradually declined and Northern Hemisphere glaciations began. A brief warming period, the early Pliocene climatic optimum, occurred from 4.5 to 3.5 Ma. At that time, Northern Hemisphere ice melted and temperatures were an estimated 2°C–4°C warmer than present in the western U.S. (Haywood et al. 2001) and as much as 19°C warmer in the Arctic (Ballantyne et al. 2010) with less seasonal, wetter climates characterized by less freezing conditions. This warm period was followed by the fluctuations of the ensuing ice ages, which started about 2.6 Ma.

By all indications, Paleogene warm, humid lowlands and the cooler uplands alike in the California region were characterized by precipitation distributed throughout the year; persistent drought was uncommon (Wolfe 1975). Even late in the Neogene, during the Pliocene, climates generally were characterized by mild seasonality, high humidity, and equable climates in western North America (Thompson 1991). Truly arid climates and dry environments did not develop until late in the Neogene, and seasonality began to appear regionally only after the Eocene-Oligocene event. The California Current, an ocean circulation pattern that exists at present, began to evolve about 15 Ma (Lyle et al. 2000). This current is a primary driver of Mediterranean climates in the California region and also regulates the steep summer thermal gradient from the coast to the interior. Loss of summer rain as a result and extension of a long summer drought became important influences on the evolution of the modern California flora. Significant regional rain shadows developed with evolution of Sierra Nevada and Basin and Range topography, marking initiation of summer-dry climates and the first appearance of desert environments. A Mediterranean climate pattern appears to have evolved in California by 7 to 4 Ma as the California Current strengthened, although some regions retained a pattern of summer precipitation (Hickey 1979, Axelrod 1988).

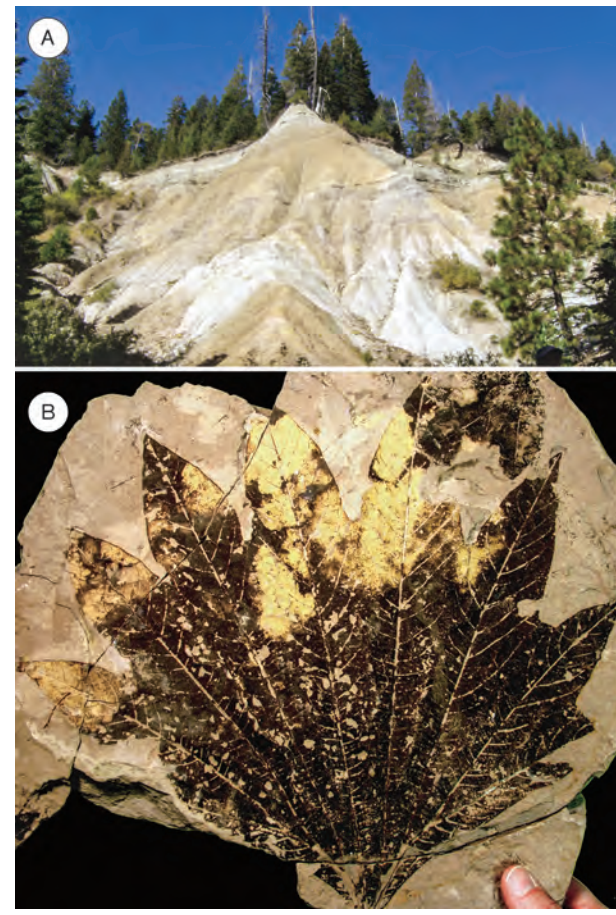

FIGURE 8.6 Eocene fossils of the northern Sierra Nevada, California. Photos: Diane M. Erwin.

A At the late Eocene LaPorte flora south of Quincy, California, sediments are exposed of a paleochannel that was part of the ancestral Yuba River system. These preserve a diversity of fossils of warm-humid tropical and subtropical plant species that were characteristic of California in the early Tertiary.

B Impression leaf fossil from another Eocene site, the Chalk Bluffs flora east of Nevada City, California, of the extinct genus *Macginitiea* (Platanaceae).

During the Paleogene and especially the Neogene, we can trace the roots of California's modern flora with satisfying detail (Millar 1996, Edwards 2004). The story of this development mirrors events in the geologic and climatic history of the interval (Wolfe and Upchurch 1986). Early in the period, species and community assemblages reflected adaptations similar to the late Mesozoic. Specifically, angiosperm and gymnosperm taxa had adaptations to conditions warmer than present and with precipitation distributed year-round (Wolfe 1985). Records from Wyoming during the PETM indicate that this hot episode created a global floristic upheaval likely experienced in California as well (Wing et al. 2005). Evidence points to massive plant species range shifts of 1,500 kilometers that occurred in less than ten thousand years in response to rapid warming. These dynamics were highly individualistic: some taxa persisted in place while others underwent significant displacement.

In California, angiosperm diversity appears to have been relatively low before 55 Ma. Fossil taxa bear scant affinity to modern lineages but show warm-temperate and some subtropical adaptations (Wolfe 1985, Axelrod 1988). Increasing temperatures and humidity ~50–52 Ma triggered significant floristic shifts toward species adapted to tropical conditions and resembling taxa now in rain forests of eastern Asia, southern Mexico, and Amazonia (Wolfe 1975, Axelrod 1988). The Chalk Bluffs fossil flora near Colfax in Nevada County, California, contains one of the richest floras in the west from this climatic period (MacGinite 1941; Figure 8.6). In it, many species belong to families long extinct in California. More than seventy-one taxa are identified, including many evergreen angiosperms and deciduous species. Few taxa overlap current native species. Five genera of laurels (including avocado, *Persea*), a palm, and a viburnum (*Viburnum*) are included, as well as now-exotic genera such as *Perminalia*, *Phytocrene,* magnolia (*Magnolia*), Spanish-cedar (*Cedrela*), *Hyperbaena,* jackfruit (*Artocarpus*), figs (*Ficus*), and *Meliosma*. Only one gymnosperm, a cycad, is present as a leaf fossil, although temperate conifers including pines, firs (*Abies*), and spruces (*Picea*) are represented by pollen. Such conifers are not recorded in other floras of this age in California. These and other taxa recorded only as pollen in these fossil beds (Leopold 1984), such as *Platycarya,* walnut (*Juglans*), hickory (*Carya*), and sweetgum (*Liquidambar*), have pollen widely dispersed by wind that may have drifted from uplands either in the Klamath or proto–Sierra Nevada ranges to the east. Warm-humid tropical adaptations are reflected in floras elsewhere in California, which had multistoried rain forests containing, for example, cinnamon (*Cinnamomum*), bay laurel (*Laurus*), walnut, magnolia, and cootie (*Zamia*), as well as rich understories and diverse ground layers (Axelrod 1988).

Whereas western California was blanketed by rich subtropical plant communities prior to about 33.5 Ma (Wolfe 1975, 1985), upland regions to the east in the Great Basin high plateau harbored refugial populations of temperate-adapted species, including many conifers and associates now present in the modern flora (Axelrod and Raven 1985, Axelrod 1988, Millar 1993, Millar 1996). These upland populations were important not only as sources for colonizing California following climatic cooling but also as sites of significant conifer evolution. Following the climatic deteriora-

tion at about 33.5 Ma, abrupt changes in floristic composition and structure took place in California. Tropical-adapted woody angiosperm species disappeared within two million years (Wolfe 1975, Wolfe 1985, Axelrod 1988). Throughout California, temperate-adapted species reappeared, especially cool-adapted, broad-leaved deciduous species and conifers (Axelrod and Raven 1985, Millar 1993), although in many cases the taxa differed from those previously present in California. These new plant communities had affinities to modern communities and high diversity, reflecting the heterogeneous climate and environmental conditions at that time. Taxa such as dawn redwood (*Metasequoia*), giant sequoia, pine, sweetgum, hickory, walnut, mountain ash (*Sorbus*), sycamore (*Platanus*), maple (*Acer*), hawthorne (*Crataegus*), elm, *Zelkova*, sumac (*Rhus*), and basswood (*Tilia*) appeared (Raven and Axelrod 1978, Edwards 2004). Notable for the first time in western records are terrestrial herb groups. Pollen records in particular document the expansion and widespread diversification of the aster family (Asteraceae) in the Oligocene. Increasing winter cold was likely a trigger for herb expansion.

Floras younger than 23 Ma include highly diverse assemblages with taxa present in California today as well as many native to climates warmer and milder than California and having year-round rainfall (Raven and Axelrod 1978). They indicate distinctions between upland vegetation and coastal communities, and reveal earliest adaptations to summer drying. During the warm climatic optimum at 17 to 15 Ma, global temperatures rose to the highest levels reached during the past twenty-three million years. Floras throughout the West from this period reflect adaptations and range shifts in response to these conditions, with increasing latitudinal gradients in composition as one moves from coastal environments to inland mountains (Raven and Axelrod 1978). Associations of taxa unknown at present persisted in many locations such as in the Tehachapi Mountains, where dry-adapted species occurred together, including Arizona cypress (*Cupressus arizonica*), Mexican pinyon pine (*Pinus cembroides*), manzanita (*Arctostaphylos*), madrone (*Arbutus*), California bay laurel (*Umbellularia*), mountain mahogany (*Cercocarpus*), several shrubby oaks, viburnum, and flannel bush (*Fremontodendron*) alongside now-exotic taxa such as figs, avocados, hopbush (*Dodonaea viscosa*), and Spanish-cedar (Axelrod 1988, Edwards 2004).

Inland, in the higher ranges of western Nevada and northeast California, fossil assemblages contained diverse conifers, including false-cypress (*Chamaecyparis*), ginkgo, fir, pine, nutmeg (*Torreya*), and hardwoods such as chestnut (*Castanea*), *Cedrella*, beech (*Fagus*), oaks, hickory, California bay laurel, redbud (*Cercis*), ash (*Fraxinus*), sycamore, cherry (*Prunus*), mountain ash, basswood, and elm in the Upper Cedarville Flora (16–15.5 Ma) (Chaney 1959); the conifers including fir, pine, false-cypress, and Brewer spruce (*Picea breweriana*), and hardwoods hickory, oak, alder (*Alnus*), birch (*Betula*), maple, sycamore, elm, and *Zelkova* in the Fingerrock Flora (15.5 Ma) (Wolfe 1964); and Arborvitae (*Thuja*), fir, spruce, pine, and giant sequoia, along with maple, barberry (*Berberis*), madrone (*Arbutus*), oak, avocado, black locust (*Robinia*), sycamore, mountain mahogany, and snowbell (*Styrax*) in the Middlegate Flora (15.5 Ma) (Axelrod 1985).

Intensification of the Mediterranean climate with decreased summer rainfall is reflected in younger floras (<7 Ma) of the California region, which have increasing representation of taxa adapted to mild and cooling temperatures with dry summers (Raven and Axelrod 1978, Axelrod 1988). These floras also show spatial partitioning of ecological communities. Increasing abundance of now-extinct horses corroborate the evolution and spread of California grasslands. A flora of this age in Contra Costa County, for example, is dominated by evergreen oaks, with abundant sycamore, cottonwood (*Populus*), willow (*Salix*), and understory taxa allied to tree poppy (*Dendromecon*), redbud, barberry, mountain mahogany, cherry, ironwood (*Lyonothamnus*), manzanita (*Arctostaphylos*), California lilac, flannel bush, sumac, and many grasses (Edwards 2004). Pollen analyzed from several long sediment cores taken at opposite ends of California corroborates these late Neogene dynamics.

Tree species no longer extant in North America remained present in the late Miocene (6 Ma) of northwest coastal California, indicating the more equable climates than modern with reduced seasonality in precipitation and temperature (Heusser 2000). After 5 Ma, arboreal hardwood and conifer species now native to the area appeared in the record, with oaks, alder, hemlock (*Tsuga*), and coast redwood dominating, and spruce at low levels (Heusser 2000). Increases in pine relative to cool, MESIC coastal forests reflected the gradual drying and warming of the continent to a thermal maximum in the mid-Pliocene (3.5–4.0 Ma). A similar pattern is documented in the latest Pliocene of Modoc Plateau (1,100 meters) in northeast California, where a long record includes pine, oak, sagebrush (*Artemisia*), cypresses (Cupressaceae), and asters at 3 Ma and is interpreted to indicate extensive forests that expanded and contracted following warm-dry and cool-wet fluctuations (Adam et al. 1989, Adam et al. 1990). Both the northwest coastal and the Modoc Plateau records document an increase in high-frequency oscillations of vegetation starting in the late Pliocene. By the close of the Neogene (~2.6 Ma), many species and vegetation elements of modern California and recognizable species affinities were in place. Here and there remained species that are exotic to the modern flora, and many locations of native species were different than at present.

The Ice Age Rollercoaster: Quaternary Environments (<2.6 Ma)

During the past 2.6 million years, tectonic changes had greatest OROGENIC impacts in eastern and southern California. Continuing Great Basin expansion and dynamics along the California Shear Zone contributed to the present topography of the southern Sierra Nevada, White Mountains, and Carson Range ESCARPMENTS. They also catalyzed development of adjacent deep and sharp-bordered basins, such as the Owens and Carson Valleys, as well as deepening of the Lake Tahoe Basin. Major volcanic events continued in California throughout the Quaternary, centered along extensive fault zones of the Sierra Nevada, Cascades, and Coast Ranges. A globally significant example is the Long Valley eruption of eastern California. Basaltic eruptions began around Long Valley about 4 Ma, coinciding with fault subsidence of Panamint Valley, Death Valley, Owens Valley, Saline Valley, and many other valleys in southeastern California.

Volcanism began in the Glass Mountains about 2 Ma and peaked in a cataclysmic eruption of 600 km^3 of high-silica rhyolite at 760 ka (Miller 1985). This massive eruption resulted in ash clouds extending as far as Nebraska and widespread deposition in California of the Bishop Tuff. Simulta-

neous 2–3 kilometer subsidence of the magma chamber roof formed the present Long Valley Caldera, the westernmost portion of which approaches the modern Sierra Nevada crest near Mammoth Lakes. Subsequent volcanism in this region shaped much of the current landscape, including, for example, Mammoth Mountain, which erupted as a series of small extrusions over a period from 110 ka to 50 ka. Volcanism shifted north, first forming the Mono–Inyo Craters chain (50 ka to 650 years before present) and then further northward to form the islands of Mono Lake, where volcanism continued to just before the historic period (about two hundred years ago) and is still active, as attested to by hot springs on the lake's islands.

The Quaternary Period is delineated mainly by climatic patterns. The general background trend starting prior to the Quaternary was toward global cooling as well as development of regions of aridity (see Figures 8.2 and 8.5). In California the Mediterranean climatic regime, with dominance of winter precipitation and dry summers, had evolved by the early Quaternary and persisted throughout the subsequent glacial and interglacial periods, although the length and intensity of the respective wet and dry seasons varied. As Earth cooled over the past four million years, and its orbital relationships intensified icehouse conditions, climate variability began to change discernibly around 2.6 Ma. Modern, high-resolution methods to detect past temperatures from stratified ice in polar ice caps and deep-ocean sediments reveal more than forty cycles of long glacial (cold) and interglacial (warm) intervals beginning about 2.6 Ma, each lasting 40,000 to 100,000 years. California appears to have experienced temperature differences as much as 7–8°C between the last glacial maximum (LGM, 20–18 ka) and present (Adam and West 1983). High-resolution analysis of ice and sediment core sections reveals that nested within these major glacial and interglacial phases were shorter repeating patterns of variability. For instance, during the last glacial interval, extreme cold periods (stadials) were regularly interrupted by shorter warmer periods (interstadials) as well as by very short reversals (fewer than a thousand years) between extreme cold and relatively warm conditions (see Figure 8.1). The cumulative effect is a sawtooth pattern typical of Quaternary climate records from around the world. An important insight from this view of the Quaternary is the overall similarity of the Holocene (formally designated as starting 11,700 years before present) to interglacial periods throughout the mid-late Pleistocene.

During glacial periods of the Quaternary, polar ice sheets expanded in Greenland and Antarctica. Continental ice sheets developed across northern North America and parts of northern Eurasia, and glaciers formed on continental mountains to the south of the ice sheets. In California glaciers formed in the Trinity Alps, Salmon Mountains, Cascade Ranges (Mount Shasta, Mount Lassen, Medicine Lake), Warner Mountains, Sweetwater Range, White Mountains, Sierra Nevada, and San Bernardino Mountains. By far the most extensive glaciations occurred in the Sierra Nevada, where during the coldest parts of glacial periods an ice cap extended over most high parts of the range. During the LGM, the Sierra Nevada ice cap was 125 kilometers long, 65 kilometers wide, and extended downslope to about 2,600 meters in elevation (Gillespie and Zehfuss 2004). Valley glaciers, fed by the ice cap, extended 65 kilometers down the west slope canyons of the Sierra Nevada and at most 30 kilometers down the shorter but steeper eastern escarpment canyons (Figure 8.7). As the mountain ranges acquired their modern geometry, glacial action in turn carved the landscape in new ways. The Quaternary glaciers of California deposited prominent MORAINES, etched glacial CIRQUES and valleys, and sculpted ARÊTES and MATTERHORN topography (see chapter lead image).

As glacial intervals waned, and the Sierra Nevada continued to be influenced by tectonic processes of tilting and subsidence, large rivers ran off both slopes, eroding deep incisions and charting new courses (Wakabayashi and Sawyer 2001). An example of the combined effect of river and glacier forces is Yosemite Valley. Deepening of the valley is attributed equally to the forces of glacial and river erosion. Widening of the valley, by contrast, is considered primarily the work of glaciers. High winter precipitation, runoff from glaciers and snow, and lower evaporative pressure from cool temperatures led to development of large lakes in the Central Valley (e.g., Lake Clyde, which filled the San Joaquin Valley 700–600 ka) (Sarna-Wojcicki 1995) and in the Great Basin (e.g., large Pleistocene versions of Mono and Owens Lakes) (Smith and Street-Perrott 1983). Feedback effects might have amplified wet conditions. For instance, water evaporating off Lake Clyde would have recharged Pacific air masses that lost water as they passed over the Coast Ranges. Additional water likely increased snowpack in the Sierra Nevada and potentially contributed to maintaining the western Great Basin PLUVIAL LAKES as well (Sarna-Wojcicki 1995, Reheis 1999).

As a result of ice buildup on land during glacial periods, global ocean levels fluctuated throughout the Quaternary, declining as much as 120 meters relative to the present during the last two glacial maxima (140 ka and 20 ka) (Inman et al. 2005, Lambeck et al. 2002). Declines of 60 meters in sea level characterized less severe stadial periods during the last two glacial cycles. Along the Pacific margin, maximum California coastline retreat at 20 ka was about 80 kilometers to a position west of the Farallon Islands that converted San Francisco Bay, Eureka Bay, and other low basins into dry land.

The present-day California Current system, which is responsible for maintaining the region's dry Mediterranean climate as well as the cool coastal fog belt, wavered in its intensity through the Quaternary (Herbert et al. 2001). When strong, as now, the California Current brought cool, relatively fresh water from the Oregon coast south along the California margin to just south of the U.S.–Mexico border. This current promotes favorable conditions for upwelling of cold water during much of the year, particularly in the summer months. During the peaks of glacial periods, however, continental ice sheets reached a large enough size to reorganize the wind systems over the North Pacific Ocean. These perturbations to wind fields caused the California Current to weaken, triggering large differences in ocean-surface temperatures relative to those of interglacial times. Collapse of the California Current during these millennia translated to weakening of the Mediterranean climate regime over California, reducing thermal gradients from coast to inland and diminishing fog belts along the California coastal zone as warmer waters came near the coast.

During interglacial periods most of these patterns reversed. As global ice melted, ocean-levels rose, coastlines moved eastward forming bays and inlets, and inland water levels lowered or dried. The oldest evidence for the San Francisco Bay estuary system is about 600 ka. At 10 ka, rising water began to fill the San Francisco Bay, which retreated partially during the middle Holocene dry and warm period, then reached a maximum extent about 4 ka (Harden 2004). The modern Sac-

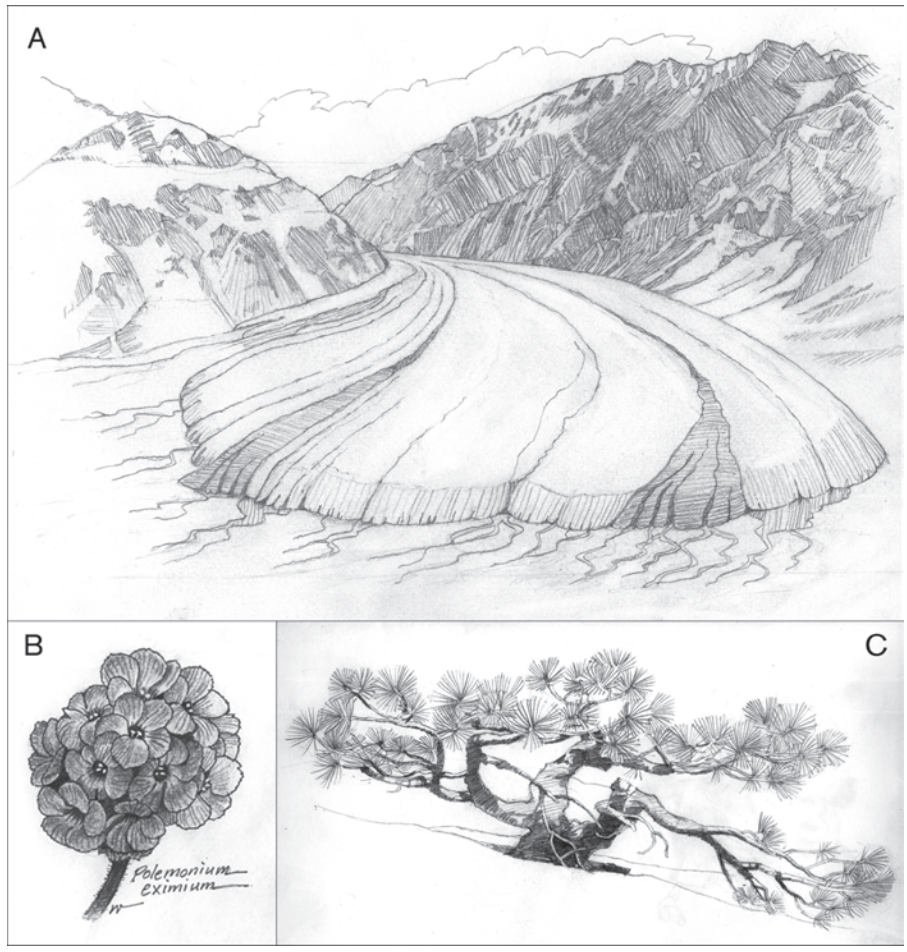

FIGURE 8.7 Pine Creek Canyon glacier at Last Glacial Maximum (20 ka), Sierra Nevada (A), and associated alpine plants skypilot (*Polemonium eximium*) (B), and whitebark pine (*Pinus albicaulis*) (C). Both species are cold-adapted and persisted in California during cold periods of the Quaternary in montane or alpine refugia, then subsequently expanded as temperatures warmed in the Holocene. Source: Artwork by Wally Woolfenden.

ramento–San Joaquin Delta formed as a consequence of postglacial sea level rise and transgression of estuarine water into the Central Valley. The California Current, with correlated summer coastal fog belt, thermal gradients, and long summer droughts, developed most strongly during peak interglacial times. The modern pattern of the current evolved about 3 ka (Herbert et al. 2001).

California plant species and communities were significantly influenced by climatic and geologic events of the Quaternary, and they responded to major and minor climate cycles. No distinct speciation or extinction events have been documented during this time in California, in contrast to abundant animal extinctions. Similarly, the major ecoregions of the state maintained species diversity throughout the Quaternary, with a few exceptions such as the extirpation of *Picea* from the Sierra Nevada, which occurred in Tahoe Basin records at 1.9 Ma (Adam 1973). Within ecoregions, however, species shifted greatly and community assemblages reflected movements of individual species across the landscape. Significant genetic adaptations at the population level occurred. Several general categories of vegetation response to Quaternary glacial-interglacial climatic change occurred in the greater California region, described here in overview and with more detail in the next section.

Latitudinal Shifts of Distribution Ranges in Low-Relief Areas

An example of latitudinal redistribution in low-relief landscapes is single-leaf pinyon pine (*Pinus monophylla*) during the last glacial cycle. Pollen and woodrat-midden records document that single-leaf pinyon pine distribution was widespread in the late Pleistocene at the southern end of its current range, mostly south of the current Mojave and Sonoran Deserts (van Devender 1990). As climates warmed during the early Holocene, single-leaf pinyon pine migrated gradually northward and upslope in the Great Basin, reaching the northern White Mountains about 8.8 ka, the Bodies Hills north of Mono Lake about 5.0 ka, Slinkyard Valley south of Lake Tahoe at 1.4 ka, the Reno area four hundred years ago, and its current northern range limit on the west side of the Great Basin near Pyramid Lake in western Nevada three hundred years ago (Figure 8.8). In much of the Mojave Desert, late glacial woodland and shrub communities—composed of such species as Utah juniper (*Juniperus osteosperma*), single-leaf pinyon, giant sagebrush (*Artemisia tridentata*), rabbitbrush (*Ericameria* spp.), and shadscale (*Atriplex confertifolia*)—shifted in composition as a result of immigration of species at different times as the climate warmed. Cool desert species were replaced by more arid

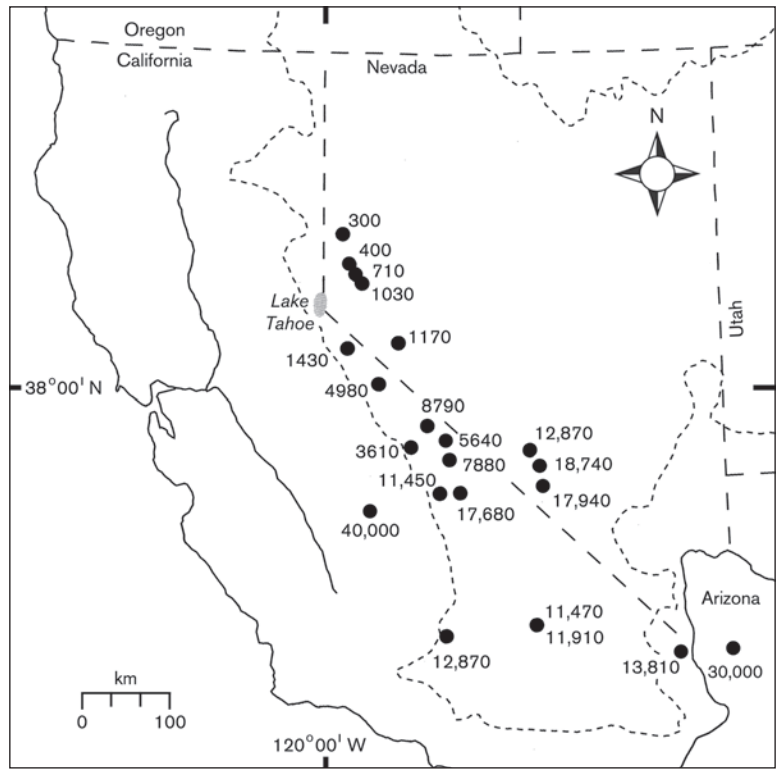

FIGURE 8.8 Movement of pinyon pine (*Pinus monophylla*) northward and upward along the western Great Basin and in southern California and western Arizona as temperatures warmed from the last glacial maximum (refugial regions in the current Mojave and Sonoran Desert regions) to its current distribution limit north of Reno near Pyramid Lake. Values indicate dates in years before present by which pinyon pine reached each point. The dotted line shows the boundary of the hydrologic Great Basin. Sites from the central and eastern Great Basin are not shown. Source: Modified with permission from Grayson 2011.

adapted species such as desert thorn (*Lycium andersonii*), rayless brittlebush (*Encelia virginenses*), and cactuses. Finally, current hot-desert adapted taxa of the present, including white bursage (*Ambrosia dumosa*) and creosote bush (*Larrea tridentata*), appeared (Spaulding 1990).

Altitudinal Shifts in Mountainous Areas

Mountains create a different kind of topographic context for species responding to climate change than do regions of low relief. Paleorecords in California document shifts in elevation that correspond to the magnitude of climatic effects of respective glacial-interglacial phases, stadial-interstadial oscillations, and centennial- to millennial-scale reversals. In the Siskiyou Mountains, for example, a record over the past fifty thousand years shows elevation shifts of 500 meters to 700 meters for tree species, with cold periods recording respective downslope movement of species in subalpine communities, mixed evergreen forests, and pine woodlands (Wanket 2002). Similarly in the southern Sierra Nevada, during coldest glacial periods when an ice cap covered the range, subalpine and montane conifer ranges shifted downslope by as much as 1,000 meters relative to their present elevations, along with similar responses by other Sierra Nevada taxa (Figure 8.9). Responses in most cases were highly individualistic and depend on the life histories and ecology of the species. Giant sequoia, for instance, appeared in packrat middens during full glacial times 700 meters below its current low elevation (1,700 meters) (Cole 1983) and might have approached as much as a 1,600 meter shift downslope (Davis 1999a). By contrast, species limited by extreme warmth and aridity during interglacials were able to expand upslope during cool stadial periods (Thompson 1988). Although major changes in species' elevation ranges occurred across climatic boundaries of the Quaternary, the changes commonly occurred at different times depending on latitude, longitude, and general elevation.

Population Contractions (Refugia and Extirpations) and Expansions (Colonizations)

Contractions and expansions were common for many California plant species in response to glacial-interglacial climate dynamics of the Quaternary. These shifts occurred sometimes with little significant change in elevational distributions. For example, coast redwood, (Poore et al. 2000, Heusser et al. 2000), the California closed-cone pines (*Pinus radiata, P. muricata*, and *P. attenuata*), coastal cypresses (*Cupressus* spp.) (Heusser and Sirocko 1997, Millar 1999), and many of California's oak species (Adam 1988, Anderson and Smith 1994) followed this pattern, contracting to fewer populations of smaller size during unfavorable periods (Figure 8.10). Such

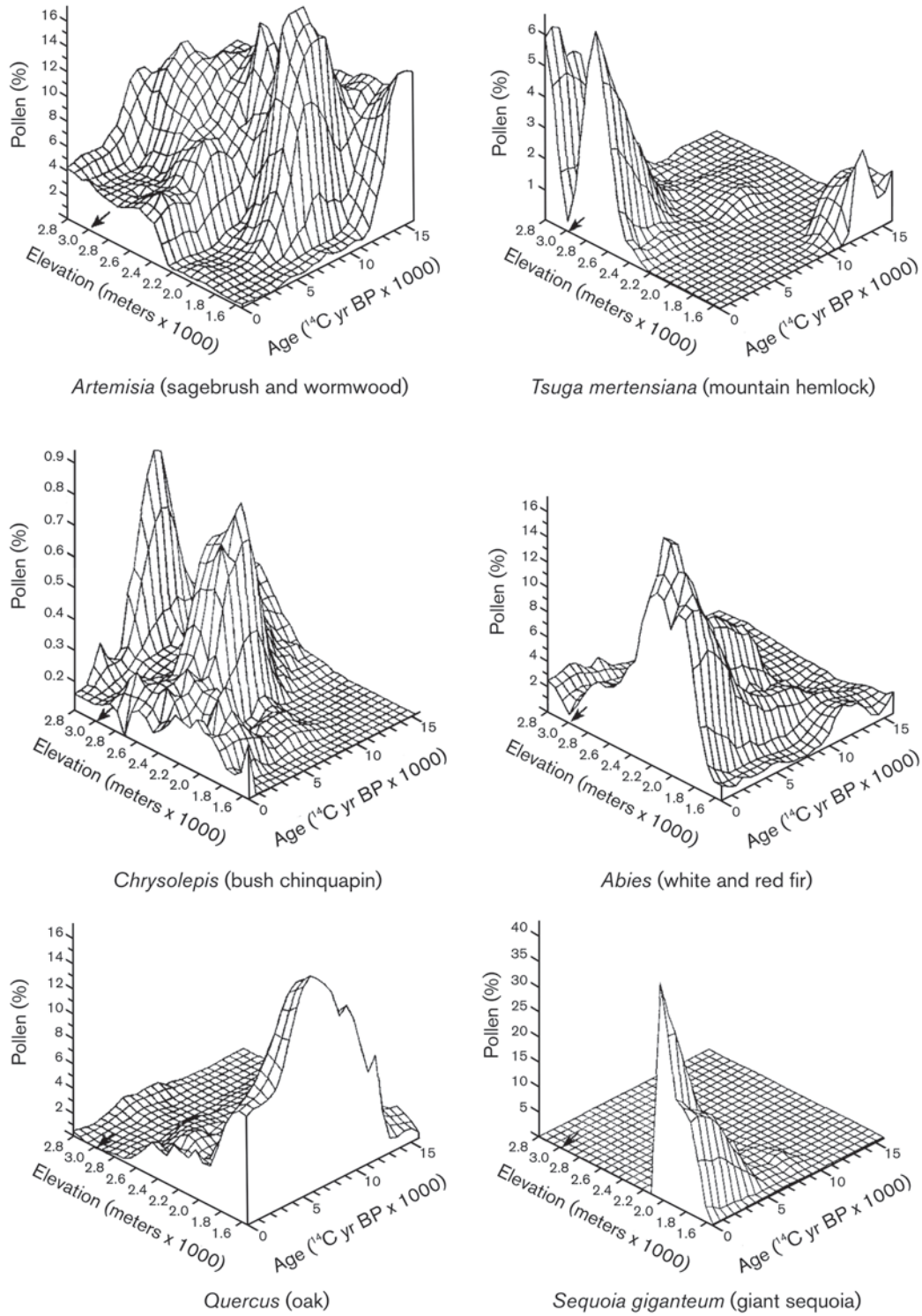

FIGURE 8.9 Schematic representation of vegetation shifts since the last glacial maximum (18 ka) in the Sierra Nevada, showing altitudinal changes as well as transmontane shifts. Values represent abundance of pollen from sediment cores at seven locations west and east of the Sierra Nevada crest (indicated by arrow). The elevation axis is from the east side (left) of the crest to the west side (right) of the range. Age is given in uncalibrated years before present (radiocarbon dates). Significant vegetation changes over time are apparent, for example, in the pattern of oak abundance, which parallels the temperature trend over the Holocene, the recent (<4,500 years) appearance and rise of giant sequoia in the western Sierra Nevada, and the recent (<5,000 years) reappearance of mountain hemlock on the west and east slopes of the range. Source: Modified from Anderson and Smith 1994.

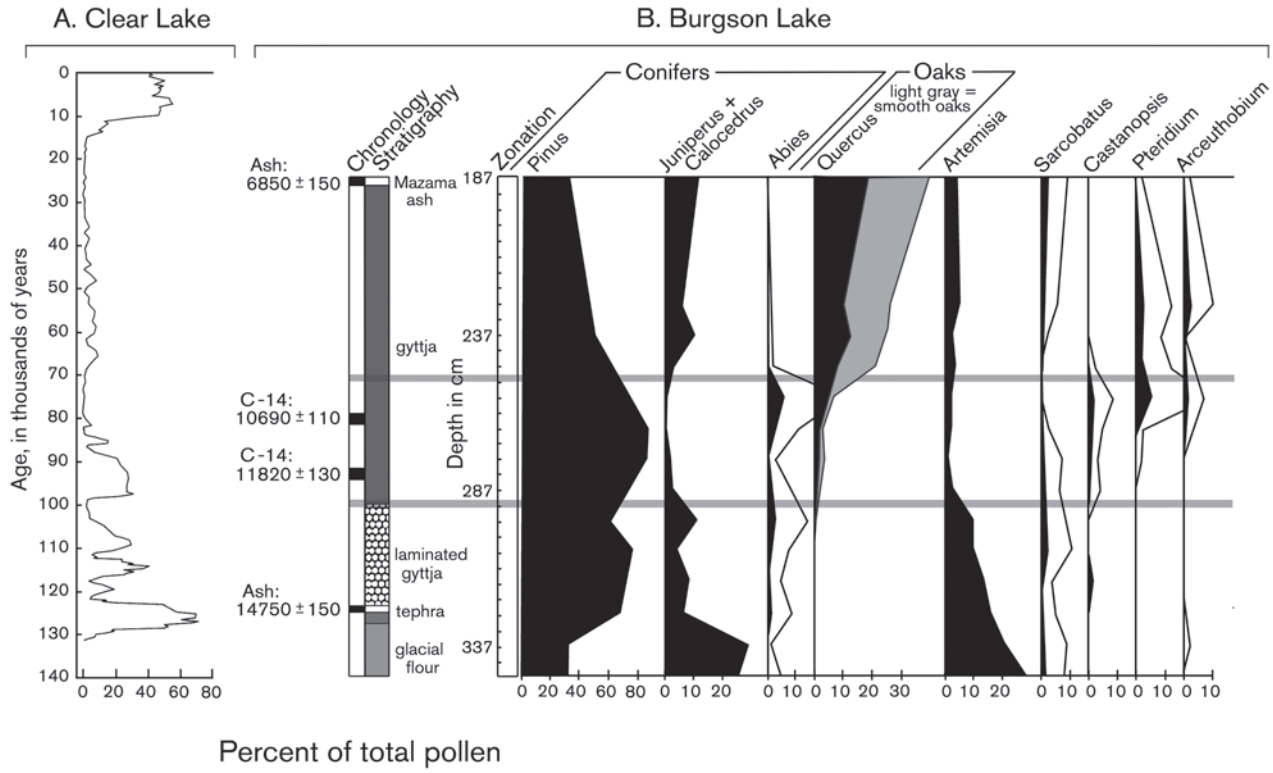

FIGURE 8.10 Pollen diagrams from Quaternary sediment cores retrieved in California.

A Percentages of oak (*Quercus*) pollen over the past 120,000 years from a Clear Lake core, Lake County. The strong correspondence (expansion/contraction) of oak abundance and temperature is shown by high pollen percentages in the Holocene, last interglacial, and interstadials of the last glacial, contrasting with low percentages during cold periods. Source: Modified from Adam 1988.

B Percentages of diverse taxa over the past 15,000 years or so from a Burgson Lake core, Sierra Nevada, showing the rapid transition at the Pleistocene-Holocene boundary. Juniper (*Juniperus*), incense-cedar (*Calocedrus*), and sagebrush (*Artemisia*) dominate in the late glacial and are replaced by oaks. The pulse of pines (*Pinus*) and fir (*Abies*) at the transition is seen in many California locations. Source: Modified from Bryne et al. 1993.

contractions rarely amounted to significant directional shift in the overall species range; rather, they caused fragmentation, loss of connectivity, and smaller population sizes. For example, California's oak populations were highly sensitive to temperature and expanded extensively during interglacials, becoming more connected and covering large areas of the California landscape. During unfavorable (glacial) climate periods, populations contracted into disjunct, isolated locations, with many population extirpations (Adam 1988, West 1993, West 1997, Mackey and Sullivan 1991, Byrne et al. 1993, Anderson and Smith 1994, Edlund 1994, Heusser 1995, Davis 1999a). Similarly, during interglacials when the California Current was strongest and coastal fog belts extensive, coast redwood expanded; the converse occurred during glacial periods (Poore et al. 2000, Heusser et al. 2000). Records in central California document rapid contractions then expansions of pines, firs, cypresses, and incense cedar (*Calocedrus decurrens*) in response to the abrupt centennial- to millennial-length reversals that occurred at the transition from Pleistocene to Holocene (West 2001).

The scattered distributions resulting from such contractions became important refugial populations for many species during unfavorable climatic periods. These were not only sources for rapid recolonization following return to favorable conditions but also critical for conservation of population-level genetic diversity. Such refugial populations also existed throughout mountainous areas, where habitat heterogeneity provided opportunities for the maintenance of small populations.

Changes in Community Composition, Including Development of Nonanalog Assemblages

Plant communities at any time and place on the California landscape reflect to varying degrees the interaction of climate with individual species' ecologies. Equilibrium with climate is rarely reached, and each species in some degree migrates toward regions of preference as climate shifts but lags relative to its ecological niche and capacity to move. In some situations, especially for broadly adapted taxa, species with similar ecologies responded synchronously to Quaternary climatic changes, such that community compositions remained relatively consistent as species shifted. For example, species of oaks, asters, and goosefoot (Chenopodiaceae) showed rapid and consistent oscillations following millennial cold-wet reversals in the southern California coast region during the last glacial and last interglacial periods (Heusser 2000). In other cases, however, species responded individualistically, and community compositions changed over time. Unusual assemblages, called nonanalog communities and created by co-occurrences of species not found together at present, resulted from unique combinations of climate, environmental conditions, species adaptation, differential migration, and

chance events. One example is a glacial (31.5 ka) assemblage north of Owens Lake in eastern California where Utah juniper and Joshua tree (*Yucca brevifolia*) grew together with an understory of giant sagebrush, bitterbrush (*Purshia tridentata*), and shadscale (Koehler and Anderson 1995). On the west side of the southern Sierra Nevada in lower Kings Canyon, a unique community comprising Utah juniper, red fir (*Abies magnifica*), incense cedar, sugar pine (*Pinus lambertiana*), and ponderosa pine (*P. ponderosa*) grew during the last glaciation (Cole 1983).

Zooming In: Retreat from the Last Ice Age (~20 ka to present)

The final development of contemporary California ecosystems traces through events that occurred over the past twenty thousand years—that is, since the LGM. Modern plant taxa were in the California region by that time, entrenched by LGM conditions into favorable ice-age environments, and poised to respond to the warmth of the new interglacial (the Holocene) that was about to ensue. From the vantage of the Holocene, and from the perspective of humans in the New World, the warm and generally ice-free environment that we know seems like "preferred" habitat for plants, rather than the colder and more arid conditions of the glacial intervals. This is a biased view, of course, for conditions of many cooler periods were more optimal for plant expansion than at present, whereas many conditions of the Holocene in California exert severe climatic stress, such as extreme aridity of the low deserts and the long drought of Mediterranean summers. Ultimately it depends on the adaptations of individual taxa, their capacities to move and to adapt genetically, that determines range distributions and community types at any one time. As summarized in the last section, transitions between glacial and interglacial periods, and the climates of interglacials themselves, were anything but gradual, directional, or stable. Rather, this time period was characterized by reversals, step changes, and low-to-high frequency variability.

Next we describe general trends of vegetation history by geographic sections of California in three times slices since the LGM. For each time period, we sweep through the state from the northwest coastal and mountain regions, southward along the coast and coast ranges, then to the Central Valley, on through the low deserts, and finally to the Sierra Nevada/southern Cascades and western Great Basin/Modoc Plateau. We generalize the vegetation stories based on the number and locations of paleo-sites available to characterize them.

Late Pleistocene (20–11 ka)

Throughout California, late Pleistocene environments were conditioned by climates that were as much as 8–10°C cooler relative to modern and confronted with warming that included a number of reversals to near-full glacial conditions. In northwest California, mountains at the current upper elevation of the mixed evergreen forest (1,200 meters), forests grew that were typical of the northern Cascades Mountains, comprising mountain hemlock, western hemlock (*Tsuga heterophylla*), spruce, pine, and fir. No records of the current forest taxa, such as Douglas-fir, oak, and tanoak (*Lithocarpus densiflorus*), were evident. Early vegetation was typical of conditions much colder and drier than currently exist. At 1,600 meters, vegetation was dominated by sagebrush, pine, spruce, and cedar likely with low fire frequencies, becoming more temperate with the arrival of Douglas-fir (*Pseudotsuga menziesii*) and firs more than five thousand years later (Briles et al. 2005). Above 1,800 meters, sagebrush and grasses composed open subalpine parklands (Daniels et al. 2005, Mohr et al. 2000).

Farther south in the lowland interior of the north Coast Range (e.g., Clear Lake at 400 meters), dense LGM forests were coniferous and comprised pines, firs, cypress, and incense cedar (Adam 1988, West 2001). The high-resolution record from this region suggests a pattern that likely occurred elsewhere, namely of high frequency replacements of the cold coniferous forest with oak-dominated woodlands and vice versa (West 2001). These are interpreted as responses to the abrupt climatic oscillations of the late Pleistocene, such the Younger Dryas cold interval, which lasted for only about eight hundred years. Evidence coastward from this region and north of the San Francisco Bay (the Point Reyes area) indicate late Pleistocene forests were more typical of modern forests about 30 kilometers north of the site, dominated by Douglas-fir and fir species (Generaux et al. 2003) and possibly with spruce (Bergquist 1977, 1978).

In the southern coastal region, LGM pollen records indicate forests that were characterized by conifers and included pine and juniper-cypress, with small amounts of oak or chaparral taxa (Heusser 1995, 1998). Similar but drier ecosystems are recorded for the LGM in the interior south coast ranges. For instance, at Carrizo Plain, pine, sagebrush, juniper, and shadscale grew (Negrini et al. 2007). Charcoal evidence also suggests fire was present in these ecosystems. During the late Pleistocene (14 ka to 11 ka) abrupt transitions along the coast occurred, starting with extreme reduction in junipers and increase in oak and chaparral taxa. During this transition, short two-hundred- to five-hundred-year periods of pine dominance occurred, which have been linked to global cold events (Heinrich events) (Heusser and Sirocko 1997). The pine component likely was dominated by one or more species of the California closed-cone pine group, which are interpreted to have expanded locally elsewhere across the California coast during the cool intervals and contracted when conditions warmed, both between the cold stadials and as Holocene conditions prevailed (Axelrod 1980, Millar 1999).

The late glacial period in the Central Valley was cold and mostly wet. Pines, firs, junipers, and alders spread in the Sacramento region, as well as members of the rose (Rosaceae) and grass (Poaceae) families, while oaks were at very low levels (West 1997). Some wetland or riparian taxa including sedges (Cyperaceae) and willows were present, likely along the major water courses. Along the southern San Joaquin Valley at Tulare Lake, records show late glacial vegetation to include tree taxa that had retreated downslope from the western Sierra Nevada in response to cold and drying climates. Cupressaceous taxa, most likely juniper, grew in the region, along with pines, oaks, sagebrush, and greasewood (*Sacrobatus*), suggesting that a pinyon-juniper woodland with halophytes grew along shallow water bodies (Davis 1999a). The presence of giant sequoia pollen through the late glacial in Tulare Lake records was originally interpreted to indicate occurrence of that conifer at 54 meter elevation in the San Joaquin Valley. More likely, giant sequoia grew in riparian forests of the low western Sierra Nevada, and pollen was washed into Tulare Lake.

For the southern deserts, between 18–12 ka, the present Mojave Desert region supported much more cool-mesic and woodland vegetation. Below 1,000 meters, Utah juniper extended through the lowlands, grading to pinyon-juniper

woodlands on the fans above (Spaulding 1990). Limber pine and bristlecone pine forests expanded during the cool LGM climates across uplands of the Mojave region. In adjacent regions now the Sonoran Desert, late glacial vegetation was very different from present, with pinyon pine on the upper slopes, while at lower elevations (<350 meters) California juniper (*Juniperus californica*), Joshua tree, whipple yucca (*Yucca whipplei*), bigelow beargrass (*Nolina bigelovii*), and Mojave sage (*Salvia mohavensis*) grew abundantly, with traces of big sagebrush, shadscale, and blackbrush (*Coleogyne ramosissima*) also present (van Devender 1990).

The late glacial vegetation of the mountains and steppelands of eastern California (Sierra Nevada, southern Cascades, Modoc Plateau, and western Great Basin) was affected by the extensive ice cap on the Sierra Nevada. This not only displaced vegetation to exposed land below the ice but also enforced cold-arid conditions, likely with dry winds emanating from the ice cap. Around the southern Owens Valley, Utah juniper was expansive, with pinyon pine also co-occurring, all at levels as much as 600 meters below their present lower treelines. Pollen in a highly resolved pollen core from Owens Lake suggests that subalpine limber pine and bristlecone pines were more extensive on the slopes of the White Mountains and Sierra Nevada than at present, and other montane and subalpine species such as foxtail pine (*Pinus balfouriana*), western white pine (*P. monticola*), and whitebark pine (*P. albicaulis*) also grew, likely in warmer niches along the mid-lower slopes (Woolfenden 2003).

On the western slopes of the southern to central Sierra Nevada, records similarly indicate reduced forest elevation ranges during the late glacial interval. At 920–1,270 meters in Kings Canyon, for instance, Utah juniper grew with red fir, incense cedar, sugar pine, and ponderosa pine (Cole 1983). Sagebrush was dominant in this region at locations around the edges of the ice cap, reflecting the cool, dry climate. Giant sequoias were more extensive in the late glacial period than present, growing at least as low at 920 meters (Cole 1983, Koehler and Anderson 1994). Extending north on the west slope to the Tahoe Basin, cold, dry climates supported open conifer woodlands with pine, juniper, and sagebrush-grass associations (Davis et al. 1985, Byrne et al. 1993, Mackey and Sullivan 1991, Koehler and Anderson 1994, Power 1998). On the east side of the range in central latitudes, the few available records suggest that newly deglaciated areas presently in the upper montane mixed forest zone (e.g., at 2,800 meters above Mammoth Lakes) supported cold-adapted colonizers and were mostly treeless but included sagebrush and limber pine in warmer niches (Anderson 1990). A pollen core taken from Mono Lake includes high enough percentages of giant sequoia pollen to suggest that the species was growing nearby in the late glacial period (Davis 1999b). The limited records from the southern Cascades and Modoc regions show trends similar to the Sierra Nevada for late glacial vegetation. Within what is now Lassen Volcanic National Park, sagebrush steppe grew in areas now supporting montane mixed conifer forest (West 2004). The cold continental climates of late glacial Modoc Plateau supported extensive juniper forests, scant oaks, and sagebrush steppe (Adam et al. 1989, Adam et al. 1990).

Early Holocene (11–6ka)

Dramatic shifts in climate that marked the global transition at the Pleistocene-Holocene boundary drove abrupt changes in California vegetation. Rapid warming spread after 11 ka, with short reversals in temperature back to cool climes in the latest Pleistocene/early Holocene, then rewarming to reach maximum Holocene warmth and associated drying by about 8 ka to 6 ka. In the northwest California mountains the early Holocene transition was marked by late Pleistocene subalpine forests being replaced within a few hundred years by dense pine and fir forests, which then disappeared a thousand years later (Wanket 2002). This period coincides with the globally recognized cool interval known as the Younger Dryas. As climates rewarmed at the end of the Younger Dryas in northwest California, pine, cedar, Douglas-fir, oaks, and tanoak forests spread in the uplands (Wanket 2002, Briles et al. 2005). Throughout this region charcoal evidence suggested increase in fire events as forests closed and became denser in the early Holocene. Dry-adapted chaparral shrublands expanded from northwest California north into Washington (Detling 1961). Warming and drying toward the middle Holocene drove the expansion of pines, oaks, and dry-adapted herbs, while along the coastal regions, redwood and western red cedar (*Thuja plicata*) declined (Heusser and Barron 2002). Summer drought and low annual precipitation were established by 8 ka, and with this, high fire frequencies in ecosystems dominated by pine, cedar (likely incense-cedar), oaks, and grasses. Similar pine-oak dominated forests appear in records from other northwest California sites, pointing to warm-adapted ecosystems. Farther south at Clear Lake, temperature proxies confirm that mean mid-Holocene temperatures were as much as 1–2°C warmer than today (Adam and West 1983) with surrounding vegetation dominated by warm-adapted chaparral species.

Similar vegetation shifts at the Pleistocene-Holocene boundary appear along the central and southern California coasts, with rapid declines in conifers and increases in oak woodlands, chaparral, and coastal sage scrub ecosystems (Heusser 1995, 1998). No evidence for western hemlock or coast redwood appears along the south coast during any interval of this time, suggesting that these taxa had late Quaternary southern limits on the coast at about 35°N (Heusser and Sirocko 1997). On the Channel Islands, pine and cypress forests that had characterized the island uplands during the late glacial declined dramatically and were replaced by about 11,800 years ago almost completely by coastal sage scrub and grassland (Anderson et al. 2010). As climates became warmer and drier, especially after about 9,150 years ago, sage scrub expanded and members of the rose and sunflower family became more abundant in the record (Erlandson et al. 1996).

In the Central Valley, warming global temperatures with sea level rise caused transgression of estuarine water into the Sacramento–San Joaquin Delta area (Malamud-Roam et al. 2007). This no doubt affected the nature of ecosystems, favoring aquatic and marsh species and reducing upland species as much or more than direct climate effects did. In the southern San Joaquin Valley, the cold-adapted and coniferous late glacial forests and woodlands were replaced by pine and oak species by about 8 ka (Davis 1999a). As sagebrush declined, taxa in the goosefoot and aster families increased. High charcoal values also suggest increases in wildfires during the early to middle Holocene. The southern desert records show successive stages of transition during the end of the Pleistocene indicative of cool species moving upslope and warm-arid desert taxa moving in. The Mojave Desert ecosystem shifted, depending on location, first with pinyon decline, then retreat of juniper, to desert scrub communities that vari-

ably included shadscale, bitterbrush, indigo bush (*Psorothamnus*), white bursage, and goldenbush (*Ericameria linearifolia*) by about 8 ka (Wells and Woodcock 1985, Woodcock 1986, Spaulding 1990, Koehler et al. 2005). In the Sonoran Desert regions, vegetation shifted stepwise from extensive cool late glacial woodlands and shrublands of pinyon pine–California juniper through cool desert shrubs such as sagebrush, rabbitbrush, and shadscale to more arid-adapted Mormon tea, Joshua tree, desert thorn, creosote bush, and cactus by about 7 ka (Spaulding 1990).

Many changes characterized the complex topography of the eastern California mountains during the early to middle Holocene. In the eastern Sierra Nevada/Owens Valley/White Mountains region, postglacial vegetation changed rapidly from juniper-dominated basins with subalpine conifers on the low slopes to warm-dry adapted woody shrubs including mountain mahogany and pine and fir forests above (Woolfenden 2003, Koehler and Anderson 1994, Koehler and Anderson 1995, Jennings and Elliott-Fisk 1993). Xeric species of winterfat (*Krascheninnikovia lanata*), rabbitbrush, spiny hopsage (*Grayia spinosa*), and wolfberry spread into the basins by 8.7 ka. Subalpine conifers (e.g., limber and bristlecone pines, *Pinus flexilis* and *Pinus longaeva*, respectively) retreated upslope with warming, as did the pinyon-juniper woodland belt, attaining treelines near and above present locations by 6 ka (Jennings and Elliot-Fisk 1993, La Marche 1973).

At higher elevations in the central eastern Sierra Nevada, warming temperatures and the retreating ice cap exposed abundant flat and low-gradient environments that supported the widespread development of wet meadows, dominated by wetland-adapted taxa and surrounded, varying with location, by alpine shrubs or by limber and lodgepole pine forests (*Pinus contorta*) (Byrne et al. 1979, Anderson 1990). Cold-dry ecosystems, such as sagebrush steppe, were replaced by coniferous forests; hemlock appeared and rose in abundance for a short period around 9 ka. At more mesic locations, subalpine tree species currently growing in the high Sierra appeared, including western white pine, western juniper (*Juniperus occidentalis*), red fir, mountain hemlock, and whitebark pine, although by 6 ka both upper and lower treelines were higher than at present (Anderson 1990, Power 1998).

On the Sierra Nevada west slope, early and middle Holocene ecosystems developed in response to background climatic transitions from cold-dry, continental glacial conditions to warm-dry environments by 6 ka (see Figures 8.9 and 8.10). As sagebrush steppe declined and closed, mixed coniferous forests expanded in response to warming and increased effective moisture (Smith and Anderson 1992), and a pulse of high fir abundance occurred in many records. This is interpreted as a transitional effect from cold and dry environments to more open and xeric ecosystems common in the mid-Holocene. High fire frequencies also characterized this interval (Edlund and Byrne 1991, Edlund 1994, Anderson and Smith 1994). The condition of dense forests with abundant fir and incense cedar and high fire frequencies of the early and middle Holocene has been compared to the late-twentieth-century situation in California forests. In the latter case, dense forests with high fir and incense cedar and high fire occurrence have developed in response to warming and anthropogenic fire suppression. By the middle Holocene, records from the west slope montane and subalpine elevations show loss of mesic and cold-adapted species. With warming and drying, montane and subalpine meadows that had developed in the late Pleistocene and early Holocene dried and were converted to forest, mostly lodgepole pine (Wood 1975, Anderson 1990, Koehler and Anderson 1995). This situation also is reminiscent of the succession from meadow to forest that is ongoing at present in response to late-twentieth-century warming.

In the northern mountains of the California Cascades and the Modoc Plateau, cold glacial steppe ecosystems converted to forest during the early Holocene. Abrupt transitions in fewer than five hundred years occurred from steppe to fir forest in the southern Cascades (West 2004). Increases of pine, more open, parklike forests, and higher upper treeline by the middle Holocene reflect generally warm and dry climates, even at higher elevations (Starratt et al. 2003, West et al. 2007). Fire rose in importance in the Modoc region in the early and middle Holocene, as indicated by frequent fire events recorded at wetland marshes (West and McGuire 2004).

Late Holocene (<6 ka)

The long-term warming trend of the early Holocene culminated during the middle millennia (8–6 ka) with maximum heat and aridity. Across California, ecosystems shifted in diversity and composition in response to these conditions. After about 6 ka, changes in insolation contributed to the reversal of early Holocene temperatures trends and, as elsewhere, the California region began to cool. As in the early Holocene, this was not a monotonic trend. Rather, cooling was interrupted by decade- to century-scale warm intervals as well as by variability at multiple scales in precipitation and soil-moisture relations. Starting about 4 ka, a widespread cool and wet period known as the Neoglacial developed, which drove return of glaciers in the high mountains and high lake levels throughout the region. These cooling trends—interrupted by warm intervals—triggered pervasive changes in California ecosystems, culminating in the development of modern floristic diversity.

Along the northwestern California coast and mountains, cooling after 6 ka influenced the resurgence of maritime conifers forests, including expansion of redwood, fir, spruce, and alder along the coast (Heusser and Barron 2002). At mid-montane elevations inland, pine and oak decreased in extent while Douglas-fir, tanoak, and oaks increased (Briles et al. 2005, Wanket 2002). At higher elevations, oak declined while fir, hemlock, and pine increased (West 1989, West 1990, Mohr et al. 2000, Wanket 2002, Daniels et al. 2005). Decreasing oak abundance in the Clear Lake region reflects response to declines of 1°C to 2°C after the middle Holocene (Adam and West 1983). Recorded along the southern coast are indications that high-frequency variability developed during the late Holocene, with an increase in extreme El Niño events alternating with droughts (Heusser and Sirocko 1997, Anderson 2002). On the Channel Islands, grasslands replaced sage scrub after 6,900 years ago, and wetland plants became prominent after 4,500 years ago, suggesting transition toward a cooler, wetter climate (Anderson et al. 2010).

Records are slim for the late Holocene in the Central Valley. Tree-ring and diatom reconstructions of streamflow provide evidence for regional trends toward cooling and mesic conditions over the past four thousand years (Malamud-Roam et al. 2007). Especially in the early portion of this interval, these led overall to higher flows and pulses of greater freshwater than modern values (Meko 2001, Meko et al. 2001, Stahle et al. 2001, Byrne et al. 2001, Starratt 2002). These records also

show periods of drought, in some intervals correlating with hemispheric warm periods and others not (e.g., the Medieval period). In the southern San Joaquin Valley, cool and moist conditions developed after 4 ka, triggering declines of xerophytic shrub communities and taxa such as greasewood (Davis 1999a) and raising lake levels during the thirteenth through the eighteenth centuries (Negrini 2013). Higher fire frequencies relative to the mid-Holocene suggest that valley woodlands and shrublands developed sufficient fuel and cover to carry range fires.

The cool and moist conditions of the Neopluvial, a cold and wet episode 2–4 ka, correlated with expansion in the southern deserts of California of relatively mesic species such as blackbrush, Mojave sage (*Salvia mohavensis*), and goldenbush (Enzel et al. 1992, van Devender 1990). In other parts of the Mojave and Sonoran Deserts, modern desert taxa such as creosote bush, ironwood, ocotillo (*Fouquieria splendens*), and white bursage expanded after 6 ka, in some situations arriving only in the last millennium (van Devender 1990, Spaulding 1990). During the cool and wet Little Ice Age (1450–1920 CE [common era, equivalent to AD]) (Mann et al. 2009), shallow lakes filled currently dry desert playas, and desert montane shrub communities shifted downslope into zones now occupied by creosote bush communities (Cole and Webb 1985, Spaulding 1995, Koehler et al. 2005).

The warmth of the middle Holocene drove upslope movement of elevationally zoned vegetation in the mountains of eastern California. Bristlecone pine in the White Mountains reached its highest Holocene elevation 150 meters above mid-twentieth-century altitude at 6–4 ka, with corresponding upward shifts of the pinyon-juniper woodland (LaMarche 1973, Jennings and Elliott-Fisk 1993). Subsequently, these montane forest ecosystems retreated downslope in response to long-term cooling trends. At lower elevations in the White/Inyo Mountains, modern vegetation appears to have become established between 4–2 ka (Jennings and Elliott-Fisk 1993, Koehler and Anderson 1995, Reynolds 1996). In the uplands of the central Sierra Nevada, regional cooling and increased moisture triggered expansion of closed conifer forests that included fir, pine, and hemlock, and drove upward shifts of altitudinal ranges (see Figure 8.9; Anderson 1987 and 1990, Dull and Edlund 1997). Declines of conifer abundance in this region coincided with the warm dry Medieval Climatic Anomaly. At Whitewing Mountain (3,100 meters) north of Mammoth Lakes, a diverse conifer forest containing lodgepole pine, western white pine, sugar pine (*Pinus lambertiana*), Jeffrey pine, whitebark pine, and mountain hemlock grew in contexts currently above local treeline between 900 and 1350 CE (Millar et al. 2006), reflecting warm-dry conditions of that interval. This forest was unusual for having species not currently present in the eastern Sierra of this region. Similar altitudinal trends occurred in the southern Sierra Nevada (Graumlich and Lloyd 1996).

On the west slope of the Sierra Nevada, late Holocene records widely document declines in oak and increases in fir and incense-cedar throughout middle montane locations. Fire frequencies, which had peaked in the warm-dry mid-Holocene, also declined. Meadows expanded (Koehler and Anderson 1994), and downslope shifts appear to have occurred for fir, incense cedar, and oak forests (Davis et al. 1985). Giant sequoia groves expanded to their present abundance only within the last 4.5 ka (see Figure 8.9; Anderson and Smith 1994). Congruent records in the southern Cascades document cooling temperatures and increased effective moisture after 4–6 ka and expansion of mesic- and snow-adapted forests that included higher percentages of fir (Mohr et al. 2000). Similar trends occurred in the Modoc Plateau region, where fir pollen increased after 6 ka in the Medicine Lake area (Starratt et al. 2003), while at Tule Lake, juniper and sagebrush increased in response to inferred cool-dry conditions (Adam et al. 1989).

A significant new factor influencing vegetation patterns in California during the past ten thousand years was the presence of humans (see Chapter 10, "Indigenous California"). In the California region, Native American activity likely had its greatest effect on vegetation from 6–4 ka, as expansive migrations of people throughout California took place, populations grew, and sophisticated methods of plant use and vegetation control developed. Invasion of modern Eurasians starting in the 1700s and increasing greatly from the mid-1800s on vastly altered the scope, rate, and nature of vegetation change in the region (see Chapter 5, "Population and Land Use").

Lessons from the Past for the Future

An important message from the study of historical vegetation for resource managers, conservationists, and climate-adaptation planners is that dynamism, not ECOSYSTEM STATIONARITY (Milly et al. 2008), is the norm. Perspectives that assume static conditions as a baseline derive implicitly or explicitly from a specific time interval, usually unspecified and often too short for the processes under consideration (Lovejoy 2013). Embracing and understanding the nature of environmental change, and of interacting forces over time and at multiple scales, provides a more effective framework from which to sustain dynamic nature, protect biodiversity, and deliver ecosystem goods into the future (Jackson 1997, Willis and Birks 2006, Millar et al. 2007).

Teaching about historical dynamics and the fluidity of ecosystem change should not be mistaken as an admission that "anything goes." To the contrary, there is no question of the need to mitigate stressors such as greenhouse pollution. In the meantime, climate adaptation strategies must be actively implemented for wildland and urban ecosystems. We can benefit in these efforts by learning from stories of past ecosystems (Willis and Birks 2006). Incorporating knowledge of historical change into effective adaptive management and resilient conservation frameworks implies working with natural processes rather than against them (Jackson 1997, Millar and Woolfenden 1999, Millar and Brubaker 2006). An example of the past informing current conservation perspectives is the recognition that species often respond to natural climate change adaptively by moving geographically. Past dynamics illustrate that population extirpation on the one hand, and recruitment and spread on the other, are not necessarily ecological problems but can be the leading and trailing edges of adaptive migration. Landscape-level mortality events such as forest dieback can swiftly advance the genetic fitness of a population so as to make ecosystems more adapted to climatic (and other) conditions of the future (Rocca and Romme 2009, Kuparinen et al. 2010, Millar et al. 2012). Fragmentation of species into isolated populations as a result of changing climates can lead to extinction vortices. However, long-term adaptive resilience under rapidly changing climatic conditions of the past has often depended on the existence of disjunct refugial populations, the consequent genetic diversity that evolves in isolation, and the key role of refugia in recolonization and restoration (Araujo 2009). A climate-savvy

adaptation approach encourages managers to assess historical conditions against the contemporary situation and to consider among the array of possibilities maintaining species in environmentally appropriate refugia. The broader challenges that depart from past circumstances involve facilitating these kinds of ecological and evolutionary dynamism in the context of new stresses, like invasive species and landscape fragmentation, that can hinder adaptive ecosystem responses.

Another example of historically informed conservation is in the context of assisted migration. This climate adaptation practice remains controversial (McLachlan et al. 2007), primarily in discussion over ethical and legal issues of moving species intentionally outside currently native ranges. A long-term perspective, however, not only challenges the concept of a static current range (rather, ranges shift with time) but more importantly can provide useful information on how species migrated under specific climatic conditions of the past. This then can inform development of modern climate-adaptation plans (Millar 1998, 1999) that help overcome new barriers to movement.

A long-term (century-scale) view can also help to frame management objectives effectively. Biotic response to change over time is a "variable chasing a variable, not a constant" (Jackson 1997), so management strategies based on historical variability as a proxy for ecological sustainability can benefit from longer temporal perspectives than usually employed (Millar 2014). In ecological restoration, for instance, setting targets by reference to historical conditions is likely to lead to failure when the historical reference conditions do not resemble future regimes. Rather, aligning restoration goals with anticipated future projections is more likely to lead to success. In western North America, for example, presettlement conditions (e.g., the mid-nineteenth century) have often been used as targets for forest restoration (Morgan et al. 1994). This time period, however, was the coldest interval of the Little Ice Age; forests that established then are poor models for forests that would flourish under future warm environments.

The obstacles and impediments of the human-built landscape lack any historical analogs and are primary drivers of novel impacts to California ecosystems. While climate, with its natural and increasingly human-dominated components, interacts significantly with other stressors, the truly new threats to ecological sustainability and ecosystem services include widespread disturbances such as land use and development; greatly accelerated fragmentation of ecosystems and waterways; land, water, and air (including greenhouse gases) pollution; invasive species; and highly altered fire regimes. Conservation attention can best focus on these elements as we also assist and mimic the natural capacities of species to adapt to ongoing climate changes.

Summary

In the same way that learning details of one's family history—the environments, traditions, and lifeways of our ancestors—helps us to understand and appreciate the modern human condition, knowledge of the historical contexts of landscapes helps us to deeply understand the diversity and ecology of modern flora and fauna. This chapter narrates a story of the geologic and climatic origins of the California region, from the emergence of land out of ancient seas, through mountain-building phases, to the ongoing drama of modern geologic forces. Regional and global geologic dynamics interacted with, and influenced, the climate of the California region. Together, sequences of geologic and climatic variability influenced the rise of modern flora. Included among the lessons in this narrative is the important role of past climatic change in shaping California's vegetation, including both individual species and community associations. Past climate changes have been continuous and included many, interacting quasi-cyclic patterns with nested time scales (decadal to multi-millennial). Because California's native flora developed in the presence of dramatic climate change, many adaptations have evolved within species to cope with these pressures. Conservation and management efforts can be most successful when they work in concert with these natural adaptive mechanisms.

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Glossary

ANGIOSPERMS Flowering plants that (in contrast to gymnosperms) have seeds (ovules) enclosed in an ovary.

ARÊTE A thin ridge of rock formed between adjacent, presently, or previously glaciated valleys.

ASSISTED MIGRATION A climate-adaptation strategy wherein individuals from an actually or potentially impacted species are moved to locations projected to be climatically favorable for them in the future.

BOND CYCLES Approximately 1,000- to 1,500-year global climate cycles that alternate between warm and cool conditions and are influenced by cycles in solar activity.

CIRQUE A concave valley head bounded by steep slopes on three sides and formed by glacial activity and subsequent erosion.

ECOSYSTEM STATIONARITY An outmoded concept that ecosystems, including their components, structures, and functions, remain static over time.

EL NIÑO/LA NIÑA Also known as the El Niño Southern Oscillation (ENSO), this is a short-lived (interannual), equatorial Pacific Ocean–mediated climate regime that alternates at periods of two to seven years between winters of warm/dry and cool/wet. In California, strong El Niño years are associated with warm, wet winter whereas La Niña years are drier and often cooler.

ESCARPMENT A steep slope separating two relatively level areas and formed from fault activity and subsequent erosion.

GYMNOSPERMS A group of seed–producing plants that include conifers, cycads, and ginkgoes and are characterized by unenclosed seeds (ovules), in contrast to the enclosed seeds of flowering plants (Angiosperms).

LITTLE ICE AGE (LIA) A multicentury, late Holocene cold interval experienced widely around the world. Times varied for different regions. In California the LIA has been documented to have extended from about 1450 to 1920 CE. During the LIA, glaciers grew and advanced to their largest Holocene values. The LIA is one of several anomalous climate periods attributed to Bond cycles.

MACROFOSSIL A fossil sufficiently large to be studied and identified without a microscope.

MATTERHORN Pyramidal, in reference to a mountain shaped by glacial activity and subsequent erosion.

MEDIEVAL CLIMATIC ANOMALY (MCA) A multicentury, late Holocene anomalous climate interval experienced with varying effects in different regions of the world (some regions do not show it). In California the MCA is considered to have extended from 900 to 1350 CE, which included two long periods (200 years and 150 years) of intense drought. Some regions of California show evidence for above background mean temperatures also.

MESIC Characterized by moist conditions.

MORAINE An accumulation of soil and rock formed by glacial activity, typically along the lateral and/or lower margins of an extant or past glacier.

NONANALOG ASSEMBLAGES Historical vegetation communities that comprise species not found co-occurring at present.

OROGENIC Resulting from a mountain–building episode (an orogeny).

PACIFIC DECADAL OSCILLATION (PDO) A quasi–decade climate cycle mediated by conditions in the North Pacific Ocean that causes background climates along the Pacific coast to alternate between warm/dry and cool/moist. In California multiyear periods of so-called positive-phase PDO intensify El Niño–type weather (wet and warm), while negative-phase PDO has the opposite effect.

PLUVIAL LAKE A lake formed in a landlocked basin during times of high precipitation in glacial periods.

TAPHONOMY The study of decaying organisms over time and how they become fossilized. Also refers to conditions that affect decaying organisms as they become fossilized, especially those that alter the structure and morphology from the original (living) condition.

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